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Environmental regulation and modelling of cassava canopy conductance under drying root-zone soil water

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ABSTRACT: Sap flow was measured, with Granier-type sensors, in a crop of field-grown water-stressed cassava (*Manihot esculenta* Crantz) in Ghana, West Africa. The main objective of this study was to examine the environmental control of canopy conductance (g_c) with a view to modelling the stomatal control of water transport under water-stressed condition. Weather variables measured concurrently with sap flow were: air temperature (T_a), relative humidity (RH), wind speed (u) and solar radiation (R_s). Relationship between canopy conductance (g_c) and vapour pressure deficit (D_ε) was curvilinear while no specific pattern was observed with R_s. Average diurnal g_c decreased from 3.0 ± 0.6 to 0.7 ± 0.4 mm s^{-1} between 0730 and 2000 h local time (= GMT) each day. A Jarvis-type model, based on a set of environmental control functions, was parameterized for the cassava crop in this study. Model results demonstrated that g_c was estimated with a high degree of accuracy based on R_s, T_a, and D_ε ($r^2 = 0.92$; $F = 809.2$; $P < 0.0001$). D_ε explained about 90% ($F = 2129.7$; $P < 0.0001$) of the variations observed in g_c, whereas both R_s and T_a contributed about 2% of the explained variance in g_c. The aerodynamic conductance (g_a) was very high compared to g_c, leading to a daily average ratio $g_a/g_c > 100$ and a decoupling factor< 0.1. Cross-validation analysis revealed a consistent good performance ($r^2 > 0.85$) of the g_c model with D_ε as the only independent environmental variable. Copyright © 2007 Royal Meteorological Society

KEY WORDS cassava; sap flow; drying root-zone; canopy conductance; regulation and modelling

1. Introduction

Cassava (*Manihot esculenta* Crantz), a short-lived woody perennial tropical shrub growing between 1.0 and 3.5 m tall, is known to be highly productive under favourable conditions and produce reasonably well under adverse conditions where other crops fail. Cassava is Africa's second most important food staple, after maize, in terms of calories consumed (Nweke, 2004). Africa accounts for more than half the world's cassava production (IITA, 1997). However, most of the increases in cassava production have been due to cropland expansion, rather than increases in yield *per* hectare, as the area under production has increased by 70% in the last two decades (Hillocks, 2002). Presently, as cassava cultivation is expanding into non-traditional areas such as semi-arid regions of sub-saharan Africa (El-Sharkawy, 1993), efforts to develop high yielding and drought tolerant varieties are being advocated (El-Sharkawy, 1993, 2006; Hillocks, 2002; Nweke, 2004). For food security and environmental sustainability, future increase in cassava production should be based on alternative options other than expansion of cultivated lands as currently practised. Hence, the possibility of increasing production *per* unit land area under cultivation using supplemental irrigation or enhancing rainwater use efficiency should be exploited. However, for the purpose of precise water applications, it is essential to understand fully cassava's response to water deficit as well as to define water use and its regulations under different field conditions.

Several studies reporting the response of cassava to water stress have been carried out on plants grown in large pots in the open (El-Sharkawy and Cock, 1984; El-Sharkawy *et al.*, 1984), under a controlled environment such as screen or glass house (Alves and Setter, 2000) or under field conditions where water exclusion is artificial by covering the soil with plastic sheets (Connor *et al.*, 1981; Connor and Palta, 1981; El-Sharkawy and Cock, 1987; El-Sharkawy *et al.*, 1992; El-Sharkawy and Cadavid, 2002). The results of such experiments need confirmation and calibration for the natural environmental conditions under which plants develop. De Tafur *et al.* (1997) found that both upper canopy leaf conductance and photosynthetic rate, as measured with a portable infrared gas analyser during the dry period, of several cassava clones field-grown in seasonally dry and semi-arid locations in northern Colombia were highest at early morning and declined rapidly over the day as air humidity decreased from morning to mid-afternoon. Similarly, El-Sharkawy (1990) reported that leaf conductance and transpiration rate, as measured with a porometer during the dry period, of field-grown cassava in

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wet soil at the Colombian Eastern Plains (Los Llanos Orientales) were negatively correlated with vapour pressure deficit (D_ε) without measurable changes in bulk leaf water potential. Wind velocity of about 4 m s^{-1} also resulted in a significant decrease in leaf conductance because of the removal of the humid boundary layer over leaves, hence increasing leaf-to-air D_ε. El-Sharkawy (2005, 2006) recently reviewed and discussed the importance of field research under natural conditions to avoid plant acclimation/adaptation problems and recommended that data obtained under controlled conditions should be calibrated in the field, particularly when such data are intended to be extrapolated to field conditions or used for crop/environment modelling.

Previous studies have shown that cassava responds to drought by closing its stomata apparatus to reduce transpiration, which acts to protect leaf tissues from turgor loss and desiccation (Connor and Palta, 1981; El-Sharkawy and Cock, 1984; El-Sharkawy *et al.*, 1992; El-Sharkawy, 1993; Alves and Setter, 2000). Reductions in apparent photosynthesis and leaf transpiration have also been attributed to decreases in leaf conductance in response to increasing humidity deficit under well-watered and stressed conditions in potted plants grown outdoors as well as in field-grown crops (El-Sharkawy and Cock, 1984; El-Sharkawy, 1990, 2006; De Tafur *et al.*, 1997). The need for field studies on the response of different cassava cultivars to varying evaporative demand, particularly under limited soil water, has been proposed for identification of parental materials for developing drought-tolerant improved cultivars (El-Sharkawy *et al.*, 1984).

Measurements of single leaf conductance in most of the above studies were made with porometers and/or with infrared gas analysers that monitor both CO_2 and H_2O exchanges, which are often costly, time consuming, and present limitations for scaling to plant canopy and continuous real-time monitoring (Green and McNaughton, 1997; Lu *et al.*, 2003). Alternatively, in the present study, weather data were combined with sap flow measurement techniques to provide a low-cost option to study the effects of changing atmospheric conditions on canopy physiological response on a continuous basis. Therefore, the objective of this study was to examine the environmental control of cassava canopy conductance (g_c) with a view to modelling the stomatal control of water transport under water-stressed conditions.

2. Methods and data analysis

2.1. Study site

The experiment was conducted in a 1.2 ha field of 11-months-old cassava field with a plant density of 12 500 plants ha^{-1}, located in the *Kotokosu* watershed 15 km east of Ejura, Ghana (07°20′N, 01°16′W, 210 m above mean sea level). The cultivar is the IITA's new high-yielding Tropical Manioc Selection (TMS30572) variety with pest and disease resistant ability (O O Aina, IITA, Ibadan: personal communication), popular with farmers in Nigeria and Ghana, the two leading cassava producing countries in West Africa (Nweke, 2004). The leaf area index was measured as 3.2 ± 0.6 m^2 m^{-2} using a SunScan canopy analysis system (Delta-T Devices, Cambridge, UK). Average trunk diameter within the 48 m^2 plot was 3.4 cm. During the study the field was mainly free of weeds. The climate is tropical monsoon characterized with distinct wet (April–October) and dry (November–March) seasons. The 20-year (1973–1992) annual rainfall average is 1264 mm with an annual mean air temperature of 26.6 °C (Oguntunde *et al.*, 2004).

2.2. Weather and soil moisture measurements

Weather variables, such as incoming solar radiation (SP-LITE pyranometer, Kipp and Zonen, Delft), air temperature (50Y Temperature probe, Vaisala, Finland), relative humidity (50Y Relative Humidity, Vaisala, Finland), wind speed and direction (A100R Anemometer, Vector Instruments, UK), were sampled every ten seconds and recorded as ten-min averages with a CR10X datalogger (Campbell Scientific, Inc., USA). Incoming and reflected solar radiation was measured with a simple albedometer constructed from two pyranometers (model SP LITE, Kipp and Zonen, Delft, Netherlands) horizontally positioned 1.5 m above the plant canopy for two days. Soil moisture was routinely measured in three access tubes located in the vicinity of the cassava field. A profile probe type PR1/6 (Delta-T Devices, Cambridge, England) was used to monitor the soil water content at six different depths to 100 cm.

2.3. Sap flow measurements and analysis

Sap flow was measured within a 6×8 m^2 plot, located in the centre of the field to avoid possible edge effects, using the temperature difference method of Granier (1987). Two cylindrical probes, 2 mm in diameter, were implanted in the cassava trunks with previously installed aluminium tubes, separated vertically by 10 cm. The probes were installed on the north side of each plant, to minimize direct heating from sunshine, and then shielded with aluminium foil against rainfall, fog, dew and incident radiation. The downstream probe was continuously heated with a constant power source, while the unheated upstream probe served as a temperature reference. The dissipation of heat from the upstream heated needle increased with increasing sap flow rate. During conditions of zero sap flow, such as nighttime, the temperature difference between the lower and the upper probes represented the steady state temperature difference caused by the dissipation of heat into non-transporting sapwood. A copper-constantan thermocouple measured the temperature difference between the heated upper needle and unheated lower reference needle. Sap velocity (V, cm s^{-1}) was computed through an empirical relationship validated and confirmed for many species

(Granier, 1987; Braun and Schmid, 1999) as:

$$V = 0.0119\left(\frac{\Delta T_{\max} - \Delta T}{\Delta T}\right)^{1.231} \tag{1}$$

where ΔT is the temperature difference between the two probes and $\Delta T_{\max}$ is the baseline (maximum) temperature difference for the dataset of the day. Three representative stems were selected for sap flow gauging based on stratification of stem sizes (within the plot) into three classes. Plot transpiration (E_c), based on sap velocity of the monitored trees, was estimated as the product of weighted flow velocity and the ratio of sapwood area (A_s) and the ground area (A_g):

$$E_c = V\frac{A_s}{A_g} \tag{2}$$

Sap flow, sampled at 10-min intervals, was recorded for ten consecutive rainless days between 15 and 24 December 2002.

2.4. Canopy conductance estimation and modelling

The analysis of canopy conductance was made using the Penman–Monteith equation, which is one of the most commonly used equation (for more information on soil-water-plant-atmosphere modelling see Ritchie and Johnson, 1990), to describe the process of canopy transpiration by integrating plant physiology and environmental factors. The equation is given by:

$$\lambda E_c = \frac{\Delta A + \rho_a C_p D_\varepsilon g_a}{\Delta + \gamma[1 + g_a/g_c]} \tag{3}$$

where g_c (m s^{-1}) is the canopy conductance, Δ (kPa K^{-1}) is the rate of change of vapour pressure with temperature, γ (kPa K^{-1}) is the psychometric constant, ρ_a (kg m^{-3}) is the density of dry air, C_p is the specific heat capacity of the air (J kg^{-1} K^{-1}), D_ε is the vapour pressure deficit (kPa), g_a is the aerodynamic conductance (m s^{-1}), λ is the latent heat of water vaporization (J kg^{-1}), E_c is the canopy transpiration (kg m^{-2} s^{-1}) and A is the available energy at the canopy level (W m^{-2}). The g_c was estimated by inverting Equation (3) and substituting sap flow-based transpiration values. This represents the bulk or integrated behaviour of the leaf stomata conductance (Stewart, 1988), and is the key crop parameter reflecting its physiological response to changing atmospheric conditions. Rearranging Equation (3) gives:

$$g_c = \frac{\gamma\lambda E_c g_a}{\Delta A + \rho_a C_p D_\varepsilon g_a - \lambda(\Delta + \gamma)E_c} \tag{4}$$

where the g_a has been derived, following the formulation of Thom and Oliver (1977), as:

$$g_a = \frac{4.72\{\ln(z - d/z_0)\}^2}{1 + 0.54u} \tag{5}$$

where u is the wind speed (m s^{-1}) at the z wind measurement height (m), d (m) is the zero plane displacement estimated as $d = 0.67h_c$, with h_c as the mean crop height (m); and z_0 is the roughness length taken as $0.1h_c$. By taking the limit of infinite g_a of the Penman–Monteith equation (Monteith and Unsworth, 1990; Bosveld and Bouten, 2001), a simplified form of Equation (4) could be written as:

$$g_c = \frac{\gamma\lambda E_c}{\rho_a C_p D_\varepsilon} \tag{6}$$

Equation (6) has been shown to be valid especially when the vegetation canopy is well coupled with the atmosphere, with D_ε mainly controlling the canopy processes resulting to the decoupling factor of ≤ 0.2 (Granier *et al.*, 1996; Bosveld and Bouten, 2001). Equation (6) was tested against Equation (4) to assess how far this simplified approximation works under a water-stressed condition.

Studies have shown that g_c depends mainly on factors such as R_s, T_a, D_ε and soil moisture (Jarvis, 1976; Stewart, 1988). In the present study, the approach based on an analytical model of g_c proposed by Jarvis (1976), was parameterized. This model has been extensively used in many soil-vegetation-atmosphere-transfer (*SVAT*) schemes and is based on semi-empirical functions of stomatal control (Wright *et al.*, 1995). Stomatal conductance is often modelled as a product of response functions (f) that have values between 0 and 1 ($0 \le f \le 1$). The g_c is assumed to be determined by D_ε, T_a, and R_s according to

$$g_c = k_1 f(D_\varepsilon) f(T_a) f(R_s) \tag{7}$$

where k_1, the first model parameter, represent maximum stomatal conductance. Other control functions are:

$$f(D_\varepsilon) = \exp(-k_2 D_\varepsilon) \tag{8}$$

$$f(T_a) = \frac{(T_a - T_L)(T_H - T_a)^t}{(k_3 - T_L)(T_H - k_3)^t} \tag{9}$$

$$t = \frac{T_H - k_3}{k_3 - T_L} \tag{10}$$

$$f(R_s) = \frac{R_s}{1000}\frac{1000 + k_4}{R_s + k_4} \tag{11}$$

where T_L and T_H are the lower and upper temperature limit to transpiration fixed between 0 and 45 °C, respectively (Wright *et al.*, 1995). Parameters $k_1 - k_4$ were optimized using the Levenberg–Marquardt algorithm (Marquardt, 1963). To avoid uncertainties of using the nighttime measurements, measurements for the daytime (0800–1700 h) were used as modelling inputs. For model optimization and cross-validation, the data were divided into two equal sets: Dataset A consisted of all the odd days of measurement, while Dataset B consisted of all the even days. Dataset B was used to validate the

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model fitted on Dataset A and *vice versa*. This type of validation procedure has been described as robust and consistent (Stewart, 1988; Lu *et al.*, 2003).

3. Results

3.1. Environmental conditions, sap flow and canopy conductance

Figure 1 gives the daily rainfall total and bi-weekly profile average soil moisture from three replicates. Total rainfall amount was 52 mm for the first two months of the dry season of 2002. The scanty rains and/or crop water consumption led to declining soil water in the monitored root-zone from 0.25 to 0.13 m^3 m^{-3}. Figure 2 shows the weather data for the experimental period on a diurnal basis with the spikes representing the standard deviation from mean of ten days at a given time of the day. Daily average R_s was 205.5 Wm^{-2}, T_a was 23.9 °C, RH was 65.2% and u was 1.0 m s^{-1}.

Figure 3 presents mean diurnal sap velocity (V) and the respective standard deviations for the measurement period. V rose sharply in the morning and reached a peak around 0930 h, thereafter slightly declining until 1630 h and then decreasing to near zero with a very steep slope in the evening. The spikes show more variability during the day which seems to be consistent with the daytime variations observed in diurnal R_s (Figure 2). Figure 4 showed the observed g_c starting from early morning (0730 h) until early night-time (2000 h). Conductance (g_c) decreased from 3.0 mm s^{-1} at about 0900 h to 0.7 mm s^{-1} around 2000 h. Figure 5 shows average g_c values as a function of D_ε. The values were plotted at their mean D_ε. The spikes indicate one standard deviation from the mean value. Data were stratified into four R_s classes as shown with the legend. Similarly, average values of g_c were related to incoming solar radiation in Figure 6. The values were plotted at the average R_s value of the interval with the spikes having the same definition as above. Data were stratified into four D_ε classes. When a point is missing, no observation is present in that class. A comparison was made between g_c, estimated by Equation (4), the inverted Penman–Monteith equation, and Equation (6), the simplified form, as shown in Figure 7. Equation (6) was shown to be positively biased with 18% over-estimation of g_c, even though the predicted pattern was near perfect ($r^2 = 0.98$).

3.2. Optimization and validation of canopy conductance model

Table I shows the values derived for the model parameters ($k_1 - k_4$) and their statistics. The three stomatal control functions of R_s, D_ε and T_a explained 92% of variations in g_c with an overall error of 0.368 mm s^{-1} ($F = 809.2$; d.f. = 3471; $P < 0.0001$). By repeating the modelling exercise on two subsets (Dataset A and Dataset B), the predictive abilities are similar to the statistics estimated using the whole data (Table I). However, the contributions of both R_s and T_a to the overall explained variance of g_c is less than 2%, indicating the overriding influence of D_ε in controlling the stomata apertures. Datasets A and B were used for cross-validation of the calibrated models. The 1 : 1 plots in Figure 8 showed good agreement ($r > 0.92$) between predicted and measured g_c for the two subsets using models based on D_ε as the only independent variable.

4. Discussion and conclusions

This result showed that g_c decreased curvilinearly with increasing D_ε with higher values of g_c when $D_\varepsilon <$ 1.0 kPa. However the curves become similar when $R_s >$ 200 W m^{-2} and $D_\varepsilon > 2.0$ kPa (Figure 5). It can also be clearly deduced from Figure 6 that higher values of g_c were recorded at lower D_ε with little clear-cut relations between g_c and R_s. This may probably justify the low or insignificant contribution of R_s to the prediction of g_c as compared to D_ε. Similarly, removal of temperature function has no significant effect on the predictive ability of Equation (7). However, D_ε contributed about 90% to the explained variance in all the cases (model versions) considered (Table I). Despite little documented reports on relations between cassava canopy conductance and weather variables under field conditions, these results correlate well with findings of El-

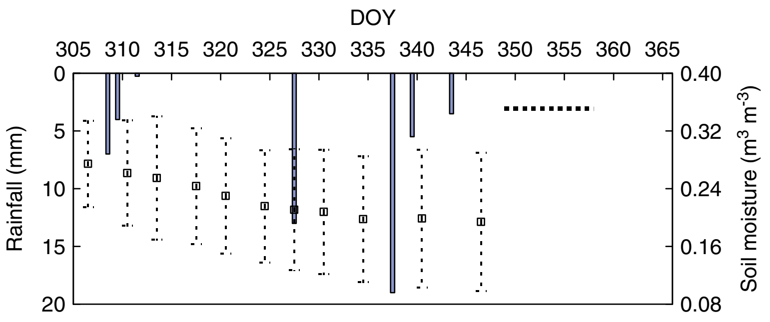

Figure 1. Average profile soil moisture (□) and daily precipitation (vertical bar) distribution (DOY = day of the year, where 1 November = day 305 and 31 December = day 365 in 2002), at Ejura, Ghana. The vertical dashed spikes are standard deviations from mean values from three access tubes. Horizontal broken bars showed the period of sap flow measurements. This figure is available in colour online at www.interscience.wiley.com/ma

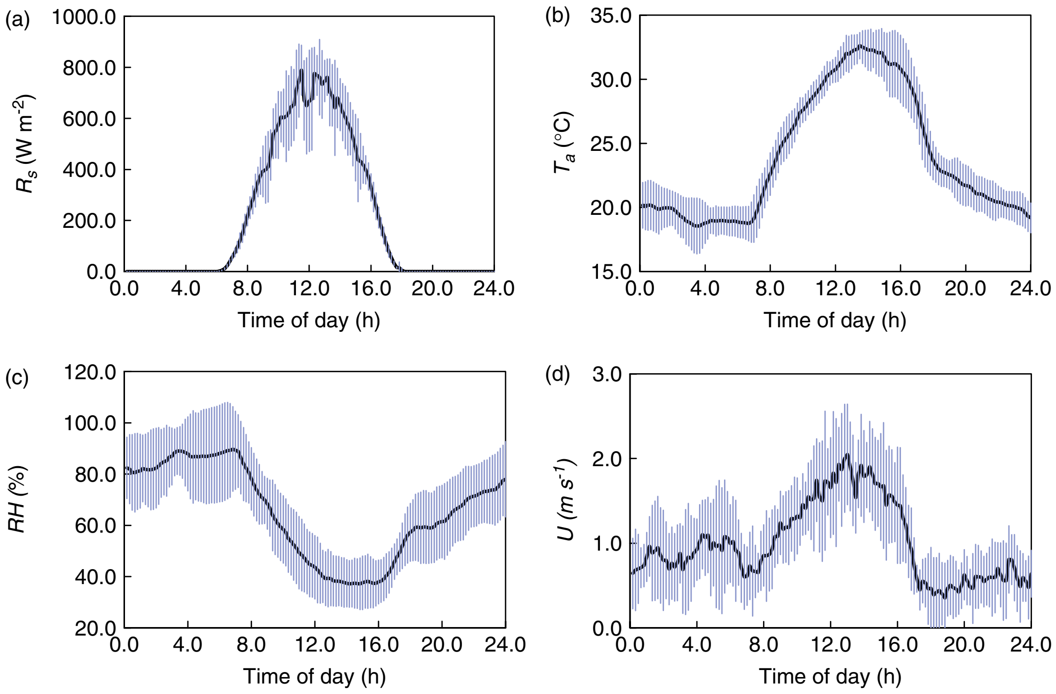

Figure 2. Mean diurnal pattern of (a) solar radiation (R_s), (b) air temperature (T_a), (c) relative humidity (RH), and (d) wind speed (u) during the ten days of sap flow measurement at Ejura, Ghana. The vertical spikes are standard deviations from mean values of respective time of the day. This figure is available in colour online at www.interscience.wiley.com/ma

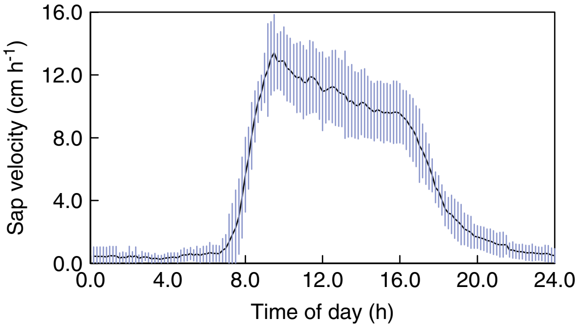

Figure 3. Mean diurnal pattern of cassava sap velocity between DOY 349 and DOY 358 in 2002. The vertical spikes are standard deviations from mean values of respective time of the day. This figure is available in colour online at www.interscience.wiley.com/ma

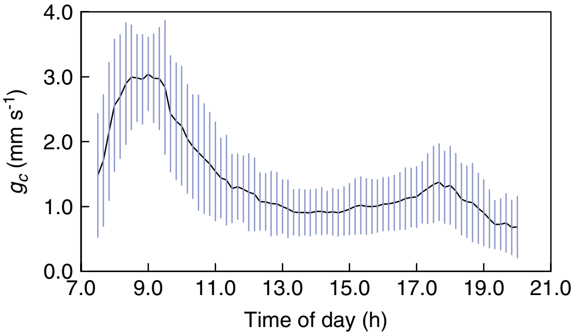

Figure 4. Mean diurnal pattern of canopy conductance (g_c) between DOY 349 and 358 in 2002. The vertical spikes are standard deviations from mean values of respective time of the day between 7:30 and 20:00 h. This figure is available in colour online at www.interscience.wiley.com/ma

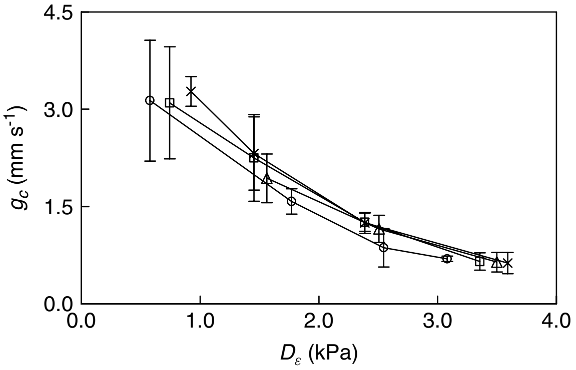

Figure 5. Effect of vapour pressure deficit (D_ε) on canopy conductance (g_c) under different classes of solar radiation ($R_s < 200$ W m^{-2} [○], $R_s = 200–400$ W m^{-2} [□], $R_s = 400–600$ W m^{-2} [x], $R_s >$ 600 W m^{-2} [△]). Point for a class is drawn at the average value of D_ε. The error bar for a class is the standard deviation from the mean of that class.

Sharkawy and Cock (1984), which were conducted in a controlled environment and at constant but high photosynthetic photon flux density. The diurnal pattern of canopy conductance (g_c) was similar to single leaf conductance of field-grown cassava reported by Connor and Palta (1981) and Cock *et al.* (1985). A sharp decline of canopy conductance (g_c) in response to increasing D_ε indicates high sensitivity of cassava leaves to changing atmospheric humidity and hence the regulation of its transpiration at the canopy level. Connor and Palta (1981) also reported the existence of significant correlation between cassava leaf conductance, as measured with porometers, and leaf-air vapour pressure deficit, with the

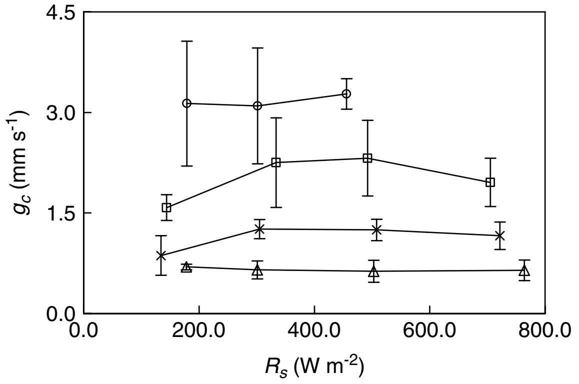

Figure 6. Observed canopy conductance (g_c) as a function of solar radiation (R_s) under different classes of vapour pressure deficit (D_ε < 1 kPa [○], $D_\varepsilon = 1–2$ kPa [□], $D_\varepsilon = 2–3$ kPa [x], $D_\varepsilon > 3$ kPa [△]). Point for a class is drawn at the average value of R_s. The error bar for a class is the standard deviation from the mean of that class.

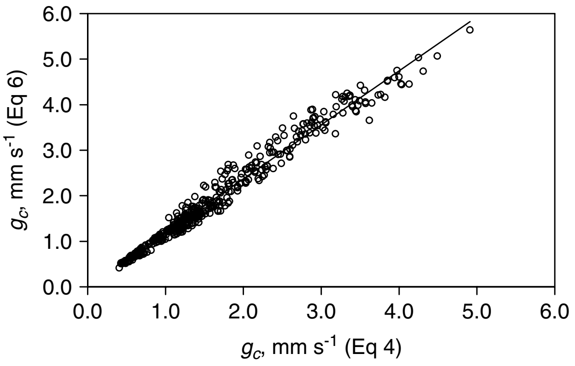

Figure 7. A simple relationship ($y = 1.18x$, $r^2 = 0.98$) between canopy conductance (g_c) estimated with Equation 4, the inverted Penman–Monteith equation, and with Equation 6, the simplified approximation.

highest correlation coefficients in the vigorous cultivar M Mex 59. In comparison with diverse species under well water conditions, the degree of stomatal response to D_ε, with a strong linear decrease, was highest in cassava (El-Sharkawy *et al.*, 1984). The curvilinear pattern observed in this study could be attributed to water shortage condition. This type of stomata response to D_ε helps cassava to avoid excessive water loss at high D_ε and becomes important strategy to survive long water-stress

Table I. Summary statistics and fitted values of parameters (± standard errors) for Jarvis-type models optimized to predict the cassava canopy conductance (g_c) with vapour pressure deficit (D_ε), solar radiation (S_R), and ambient temperature (T_a) as response functions respectively.

(a)	All data (days from 15 to 24 December, 2002), $n = 474$		
	I[1]	II	III
k_1	5.75 ± 0.33	5.44 ± 0.18	4.76 ± 0.10
k_2	0.622 ± 0.025	0.597 ± 0.015	0.562 ± 0.014
k_3	30.94 ± 2.32	–	–
k_4	34.96 ± 10.05	49.04 ± 11.09	–
r^2	0.920	0.915	0.891
Error in g_c	0.368	0.376	0.388
(b)	Dataset A (odd days from 15 to 24 December, 2002), $n = 237$		
	I	II	III
k_1	7.24 ± 0.62	6.26 ± 0.27	5.50 ± 0.14
k_2	0.725 ± 0.026	0.673 ± 0.020	0.632 ± 0.017
k_3	34.47 ± 2.74	–	–
k_4	19.96 ± 10.21	42.68 ± 12.92	–
r^2	0.934	0.919	0.911
Error in g_c	0.310	0.334	0.345
(c)	Dataset B (even days from 15 to 24 December, 2002), $n = 237$		
	I	II	III
k_1	4.83 ± 0.25	4.99 ± 0.24	4.00 ± 0.13
K_2	0.513 ± 0.032	0.539 ± 0.021	0.483 ± 0.019
K_3	26.17 ± 2.18	–	–
K_4	88.09 ± 20.48	100.76 ± 12.92	–
r^2	0.913	0.913	0.878
Error in g_c	0.346	0.353	0.385

[1] I: model with all environmental response functions, II: model excluding T_a; and III: model excluding both T_a and R_s functions. $k_1 - k_4$ are the optimized parameters (Equation 7), r^2 is variance explained.

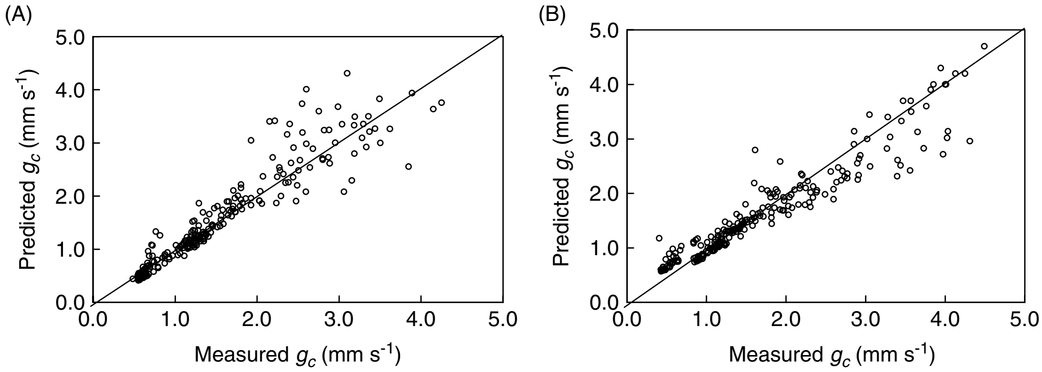

Figure 8. Relationships between predicted and observed canopy conductance (g_c). Models were cross-validated on two datasets (Dataset A – used for figure in column 2 and Dataset B – used for figure in column 1). Measured g_c of Dataset A *vs* g_c predicted from Dataset B model and *vice versa*.

situations (El-Sharkawy, 2006). However, the nature of the interactions of radiation, temperature and vapour pressure deficit and their effects on leaf and canopy conductance in the field are more complex as compared to controlled laboratory experiments. Under the laboratory controlled conditions these interacting factors are easily separated, thus leaf conductance as a function of each factor is better elucidated.

The ratio g_a/g_c was greater than 100 and the decoupling factor was estimated to be less than 0.1. These values further confirmed the very strong dependence of g_c on D_ε. Similar observations have been made in several other species (Granier *et al.*, 1996; Lu *et al.*, 2003). However, unlike in other studies in which a simplified g_c equation (Equation (6)) was found to be adequate when canopy is strongly coupled to the atmosphere, Equation (6) over-estimated g_c up to 18%, quite higher than 6% reported by Granier *et al.* (1996) and the usual 10% sap flow measurement error (Braun and Schmid, 1999; Lu *et al.*, 2003). This possibly indicates the effects of drying root-zone soil water of this field. In general, the physiological mechanisms behind the response of g_c to weather variables are very complex and still not fully understood (Jones, 1998), especially under filed conditions. Others have hypothesized the involvement of biochemical or hydraulic root signals e.g. abscisic acid (ABA) concentration (Jones, 1998; Oren *et al.*, 2001). In cassava, Alves and Setter (2000) showed that under water shortage conditions in potted greenhouse-grown cassava, ABA is rapidly accumulated in the leaves, which may also increase the sensitivity of stomata to D_ε.

In conclusion, the results of this study confirmed earlier findings and added new clear field evidence of cassava response to environment *via* a tight stomatal control at both leaf and canopy levels. The parameterized Jarvis-type g_c model is suitable for prediction of cassava transpiration under the experimental condition. This study provides further observations that may help in understanding the drought response of cassava, which are useful to evaluate/characterize the impacts of climate variability and change on crop productivity especially under sub-humid tropical environmental conditions.

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