



Whole-plant water use and canopy conductance of cassava under limited available soil water and varying evaporative demand

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Abstract

Cassava (*Manihot esculenta* Crantz), a perennial woody shrub, is known to be highly productive under favourable conditions and produce reasonably well under adverse conditions where other crops fail. Using constant heat sap flow sensors, sap flow density (F_d) of cassava was monitored for 10 days in December 2002. Sap flow was highly correlated ($R^2=0.72$, $P<0.05$) to incoming solar radiation (R_s) than to other climatic factors. Using cross-correlation analysis, no time shift was detected between F_d and solar radiation, whereas vapour pressure deficit (VPD) lags F_d by 110 min. Solar radiation and VPD together explained 83% of diurnal variation in sap flow. Whole-plant transpiration ranged from 0.8 to 1.2 mm day⁻¹ and daily canopy conductance (g_c), computed based on the inverted Penman–Monteith model, varied between 0.7 and 2.1 mm s⁻¹ (mean = 1.4 ± 0.5 mm s⁻¹). For the measurement period, characterized by high evaporative demand coupled with low available soil water, transpiration accounted for 21% of the available energy and was only able to meet 24% of the atmospheric water demand. Average decoupling factor (Ω) of 0.05 ± 0.02 estimated suggested that a 10% change in g_c may lead to more than 9% change in transpiration which further supports the notion that stomata play significant role in regulating cassava water use compared to other known mechanisms. Beyond light saturation ($R_s > 300$ W m⁻²) and at higher VPD (> 1.0 kPa), wind effects on the canopy transpiration under water stress condition were low, while VPD explains 94% of the observed variance in daily canopy conductance.

Introduction

Cassava (*Manihot esculenta* Crantz) is a short-lived perennial tropical shrub growing from about 1.0–3.5 m tall. Believed to be first domesticated in South America, its cultivation has spread throughout the humid tropics and subtropics (Rehm and Espig, 1991). Total production of cassava in

Africa has increased from 35 to 80 million tons between 1965 and 1995 (Hillocks, 2002). Africa now produces cassava more than the rest of the world combined with biggest increase from 22 to 35% (of African total production) in Nigeria and 4 to 8% in Ghana (IITA, 1997). Co-incidentally the Government of the two respective countries has introduced policies to increase cassava production for local consumption and export promotions. In 2004, a policy was initiated to produce bread with cassava-to-wheat flour ratio of 1:9 in Nigerian bakery industry. Apart from human

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food, cassava is also used for animal feed, starch and alcohol production (El-sharkawy and Cock, 1987).

Most of the increases in cassava production in Africa have been due to increases in area under cultivation, rather than increases in yield per hectare as area under production has increased by 70% in the last two decades (Hillocks, 2002). Future increase in cassava production should be based on alternative options other than unsustainable cropland expansion current practiced. Effort at development of high yielding and drought tolerant varieties is more favoured (Aina et al., 2004; Hillocks, 2002), while possibility of increasing production per unit land area under cultivation using supplemental irrigation is little exploited. However, for the purpose of precise water applications, it is essential to fully understand cassava response to water deficit and to define water use (transpiration) under different field conditions. Few publications reporting response of cassava to water stress have been carried out under artificial conditions such as screen house, containerized where water exclusion is artificial (Alves and Setter, 2000, 2004; Aina et al., 2004; Connor et al., 1981; Connor and Palta, 1981; El-sharkawy and Cock, 1984, 1987; El-sharkawy et al., 1984) warranting confirmation of the results of such experiments under natural environmental conditions under which plants develop.

Studies have shown that cassava respond to drought by closing its stomatal to reduce transpiration, which act to protect leaf tissues from turgor loss and desiccation (Alves and Setter, 2000; El-sharkawy and Cock, 1984). Reductions in apparent photosynthesis and leaf transpiration have also been attributed to decrease in leaf conductance in response to increasing humidity deficit under well-watered and stressed conditions (El-sharkawy and Cock, 1984). El-sharkawy et al. (1984) after comparing cassava's response to leaf-air vapour deficit with that of other tropical species, outlined the need for field studies on the response of different cassava cultivars to varying evaporative demand, particularly under limited soil water, because the degree of stomata sensitivity changes with growing conditions and with plant characteristics.

Measurements made in most of the above studies were conducted at 'leaf scale'. A bottom-

up approach, which is costly, time consuming, and presents difficulties for scaling and continuous real time measurements (Green and McNaughton, 1997; Lu et al., 2003). In this study, recent improvement in sap flow techniques useful for continuous monitoring of whole-plant transpiration was applied to study water relations of cassava. The aim was (1) to estimate the bulk canopy conductance of field-grown cassava by inverting the Penman–Monteith equation and (2) to characterize the response of whole-plant water use and canopy conductance to climatic factors under limited available soil water. Although this approach has been extensively used for forest and trees water relation studies, it has not been reported for cassava plant.

Materials and methods

Study site description

The study was conducted in a small watershed 15 km east of Ejura, Ghana (latitude 07°20' N, longitude 01°16' W, elevation \approx 210 m) in a 1.2 ha cassava (*Manihot esculenta* Crantz) field. 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), currently popular in Nigeria and Ghana, the two leading cassava producing countries in West Africa (Nweke, 2004). The crops were 11-month-old, planted at a plant population of 12,500 plants ha⁻¹. Experimental site lies in the forest-savannah transition zone of Ghana dominantly influenced by the tropical maritime air mass. The climate is classified as tropical monsoon characterized by distinct wet (April to October) and dry (November to March) seasons. Total rainfall in 2002 was about 1400 mm but it averaged 1264 mm between 1973 and 1992. Average air temperature for the same period is about 26.6 °C (Adu and Mensah-Ansah, 1995). A total of 52 mm of rainfall (six rain days) was recorded during the months of November and December 2002. However, no rain occurred during the observation period (Figure 1). The geological formation consists of Voltaian sandstone basin and is characterized by gently dipping or flat-bedded sandstones, shales, and mudstones

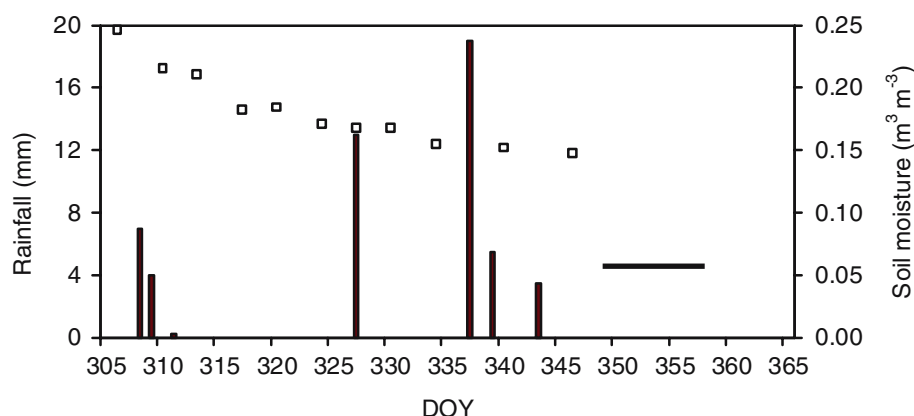


Figure 1. Profile (0.1–1.0 m) average soil moisture (\square) and daily precipitation (vertical bar) distribution for, November and December 2002, the beginning of dry season at the weather station in Ejura, Ghana. Horizontal bar showed the period of sap flow measurements.

Table 1. Instrument used for measurement of meteorology variables and soil moisture at Ejura, Ghana

Variable	Measurement height (m)	Instrument or sensor type
Solar radiation	3.5	SP-LITE pyranometer (Kipp & Zonen)
Net radiation	3.5	NR- LITE pyranometer (Kipp & Zonen)
Air temperature	2	50Y Temperature probe (Vaisala)
Relative humidity	2	50Y Relative humidity (Vaisala)
Wind speed	8	A100R Anemometer (vector instrument)
Soil moisture	-0.1, -0.2, -0.3, -0.4, -0.6, -1.0	Profile capacitance probe (Delta-T)

that are easily eroded. This has resulted in an almost flat and extensive plain, which is 60–300 m above mean sea level (Agyare, 2004). The soils in the area have a high sand content with mean values of about 72% in the topsoil (0–15 cm) and about 69% in the subsoil (30–45 cm). The textural class is sandy clay loam at both soil levels (Bates, 1962). Other cultivated crops in this area include: *Zea mays*, *Dioscorea* spp., *Vigna unguiculata*, *Magnifera indica*, *Anacardium occidentale* and *Citrus* spp.

Meteorological and soil water measurements

Weather variables were measured over grass on adjacent field about 100 m away from the experimental plot. Incoming solar radiation, net radiation, air temperature, wind speed, relative humidity and rainfall, were sampled at 10 s and recorded as 10 min averages with an automatic weather station. Soil moisture was routinely mea-

sured twice weekly until DOY 345, 2002. Delta-T PR1/6 (profile) capacitance probe (Delta-T Devices, Cambridge, England) was used in a tube located at the weather station. The sensor types used to measure the above parameters as well as the installation height above or below the land surface are given in Table 1.

Sap flow and plot-level transpiration

Sap flow measurements were made for 10 consecutive rainless days between 15 and 24 December (day of year, DOY) 349–358; Figure 1) under limited available soil water. A stratified sampling method, based on stem sizes, was used to select three representative cassava plants, with single stem per diameter-class, within a 6 m \times 8 m plot for measurement of sap flow density. Average leaf area index (LAI) was 3.2 m² m⁻² (LAI was measured at twelve points under the plants

canopy within the 48 m² plot using a canopy analysis system, LAI-2000, LiCor, Lincoln, NE), while average trunk diameter was ca. 3.4 cm.

Sap flow was measured with the temperature difference method according to Granier (1987). Two (2-cm long) cylindrical probes 2 mm in diameter, were implanted in the cassava trunks with previously installed aluminium tubes, and separated vertically by 10 cm. The probes were installed on the north side of the trees and then shielded with aluminium foil, to minimize direct heating from sunshine. The downstream probe (the upper coil) was continuously heated with a constant power source while the unheated upstream probe (the lower coil) served as a temperature reference. During conditions of zero sap flow the temperature difference between the lower and the upper probes represents the steady state temperature difference caused by the dissipation of heat into non-transporting sapwood. Sap flux density was computed with the empirical relationship validated for many species (Braun and Schmid, 1999; Granier, 1987; Lu and Chacko, 1998) as:

$$F_d = 0.714 \left(\frac{\Delta T_{\max} - \Delta T}{\Delta T} \right)^{1.231}, \quad (1)$$

where F_d is average sap flow velocity along the length of the probe (mL cm⁻² min⁻¹), ΔT is the temperature difference observed between the heated and reference needles, and ΔT_{\max} is the value of ΔT when sap flow is zero (generally taken as the peak nighttime value of ΔT). Plot-level transpiration (E_c , mm h⁻¹) was estimated from weighted averaged sap flow divided by ground area occupied by individual plant. Sap flow was derived from weighted F_d multiplied by the plot average sapwood area.

Canopy conductance and decoupling coefficient

Canopy conductance was estimated by inverting the Penman–Monteith equation

$$\lambda E_c = \frac{\Delta A + \rho C_p VPD g_a}{\Delta + \gamma [1 + g_a/g_c]}, \quad (2)$$

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 psychrometric constant, ρ (kg m⁻³) is the den-

sity of dry air, C_p is the specific heat capacity of the air (J kg⁻¹ K⁻¹), VPD (kPa) is the vapour pressure deficit, g_a (m s⁻¹) is the aerodynamic conductance calculated from wind speed using the empirical equation of Thom and Oliver (1977), 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 ($R_n - G$) at the canopy level (W m⁻²). Net radiation (R_n) and soil heat flux (G) were not directly measured over and below the cassava canopy, respectively. R_n in the cassava field was derived from measured R_s and R_n over the grass for a period of 12 days when both grass vegetation at the weather station and cassava field were having similar LAI values and reflectivity coefficients. The regression equation was found to be:

$$R_n = 0.81 * R_s - 4.65 \quad (3)$$

with $R^2 = 99$ and $n = 1728$. Daytime G was taken as 10% of estimated R_n (Phillips et al., 1997) and daily G was assumed to be zero. Ten-minutes estimates of g_c were calculated using all the variables specific to those time steps, whereas daily g_c values were based on daily averages of the relevant variables.

The extent to which canopy transpiration is controlled by stomatal aperture in response to climatic changes can be determined by a dimensionless decoupling coefficient (Ω) calculated after Monteith and Unsworth (1990) as:

$$\Omega = \frac{\Delta + \gamma}{\Delta + \gamma(1 + g_a/g_c)}. \quad (4)$$

The Ω value ranges from zero to one. Stomatal control of transpiration grows stronger as Ω get closer to zero. Simple statistical analyses carried out in this study generally include: regression, ANOVA, correlation and cross-correlation analyses. The cross-correlation function (ccf) is given as

$$R = \frac{\text{Cov}[X(t), Y(t + \tau)]}{\sigma_x \cdot \sigma_y} \quad (5)$$

i.e. the covariance of X and Y time series variables divided by the product of their standard deviations, σ_x and σ_y , respectively. The correlation between X and Y is R , t is time and τ is a lag introduced between X and Y .

Results

Climatic factors and water use

Diurnal course of major climatic factors are shown in Figure 2. Solar radiation reached a high value of 940 W m^{-2} with daytime average varying between 342 and 465 W m^{-2} , but a 24-h daily average ranged from 156 to 236 W m^{-2} . Temperature oscillated between 11.5 and $34.4 \text{ }^\circ\text{C}$ with a daily average around $24 \text{ }^\circ\text{C}$. Relative humidity varied from 100% to less than 25% with daily mean ranging from 43 to 76% . Maximum VPD was of the order of 4 kPa for all the days, though the daily average showed low values between 0.69 and 1.57 kPa . Daytime wind speed rarely exceeded 3.0 m s^{-1} , while the daily averages were generally around 1.0 m s^{-1} .

The temporal dynamic response of the measured stem flow to climatic forcing was exploited using cross-correlation analysis (Oguntunde et al., 2004). Correlations over a range of time lag -120 min to $+120 \text{ min}$, between climatic parameters and sap flow density (F_d) is presented in Table 2. For R_s versus F_d , correlation (R) ranged from 0.663 to 0.846 ; whereas R ranged from -0.252 to -0.701 for RH versus F_d , respectively. Positive lags indicate that the second variable of the listed pairs lags behind the first variable.

Diurnal patterns of sap flow (L h^{-1}) for a period of 8 days of complete 24-h records are shown in Figure 3a, while the daily water use of cassava and the prevailing potential evaporation estimated based on Penman (1948) equation are presented as bar chart in Figure 3b. Maximum rates (0.102 – 0.154 L h^{-1}) of sap flow occurred shortly after its onset in the mid-mornings of each day and were followed by continuous decrease during the rest of the day irrespective of changes in solar radiation. Plot-level transpiration for DOY 350–353 and 355 showed values $> 1.0 \text{ mm day}^{-1}$, while the remaining days were just below 0.9 mm day^{-1} . However, estimated potential evaporation, an indicator of atmospheric water demand, showed high values ranging between 3.05 and 4.98 mm day^{-1} .

A scatter plot of canopy transpiration and climatic drivers are shown in Figure 4. Highest correlation ($R=0.85$) was found between solar radiation and cassava water use compared to other climatic parameters. Obviously Figure 4

showed that the relations are generally non-linear and the observed hysteresis loops indicate the presence of phase shifts in the time series. The most successful static microclimatic model, fitted to predict plot-level transpiration, combined the parabolic response of E_c to R_s and the linear response to VPD in the form:

$$E_c = a * R_s / (b + R_s) * (1 - c * \text{VPD}), \quad (6)$$

where fitted parameters $a=0.181$, $b=267.1$ and $c=0.103$, respectively. Coefficient of determination (R^2) was 0.83 and $n=1152$.

Regulation of whole-plant transpiration

Estimated aerodynamic conductance (g_a) was generally low during the observation period due to low wind speed. Over the measuring period of 10 days, daytime g_a ranged from 85 to 236 mm s^{-1} . Canopy conductance was calculated by re-arranging Eq. (2) using the estimated plot-level transpiration data. Daytime estimated g_c between $8:00 \text{ h}$ and $16:00 \text{ h}$ (to avoid wet canopy part of the day) was correlated against R_s and VPD (Figure 5). Daytime values of g_c was between 0.4 and 4.9 mm s^{-1} (mean = $1.6 \pm 1.0 \text{ mm s}^{-1}$, $n=391$). Stomata are known to respond to light and humidity deficit. Effects of these factors were separated by plotting conductance against R_s at low values of VPD ($< 1.0 \text{ kPa}$, Figure 5b) and against VPD at high R_s values ($> 300 \text{ W m}^{-2}$, Figure 5d). The pattern shown in Figures 5a, b may be expected under stressed conditions, although g_c usually shows a hyperbolic increase with increasing radiation from unstressed plants. However, Figures 5 c, d showed a usual decrease in g_c with increasing VPD. At lower values of humidity deficit (non-limiting range), g_c declined from higher values (when $R_s < 300 \text{ W m}^{-2}$) to lower values as R_s increases. A similar situation was observed with increasing VPD under non-limiting radiation conditions.

Daily canopy conductance based on 24-h average of weather variables showed a strong exponential decrease with increased VPD ($R^2=0.94$) as shown in Figure 6. The relation between g_c and R_s showed slight decrease ($R^2=0.38$) with increased R_s . However, the large scattered points make the observed trend

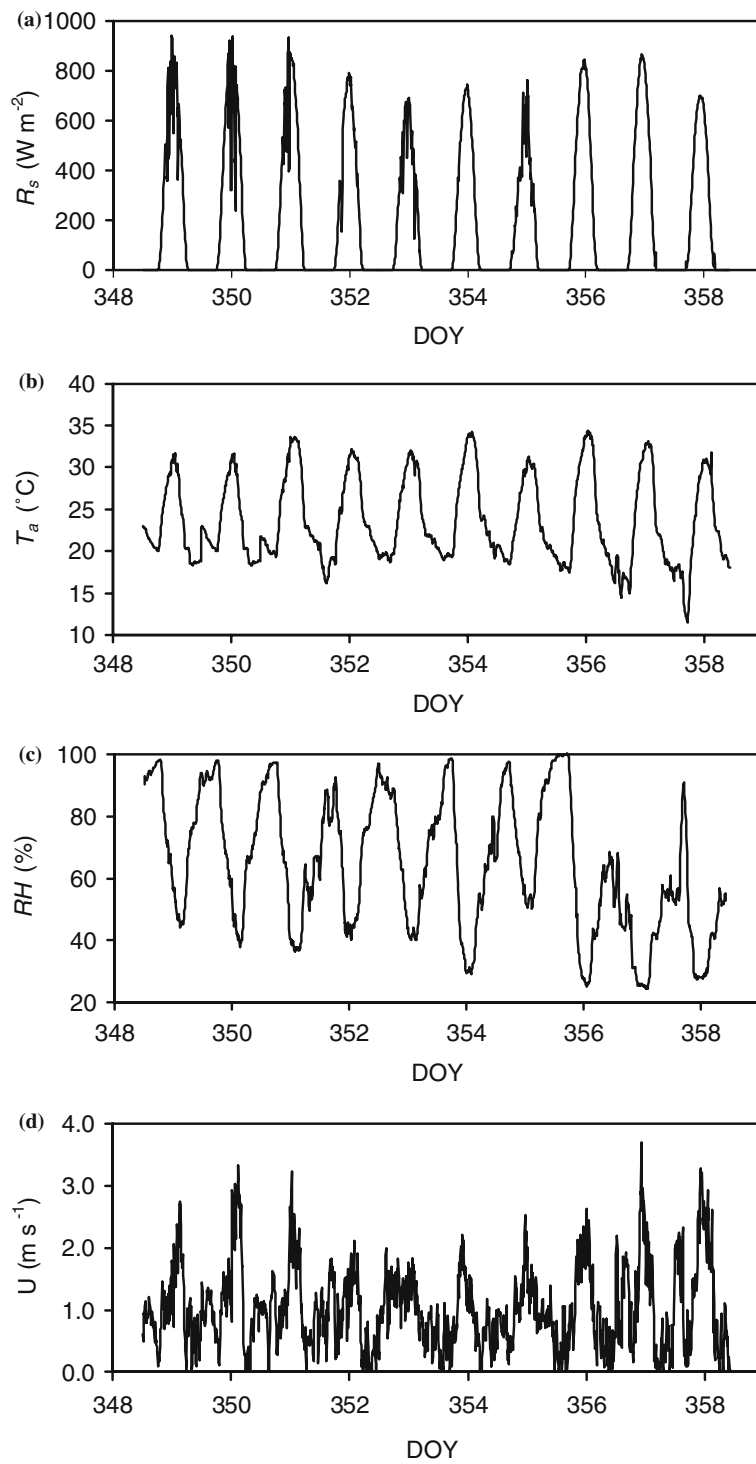


Figure 2. Diurnal pattern of (a) solar radiation (R_s), (b) air temperature (T_a), (c) relative humidity (RH), and (d) wind speed (U) during the sap flow measurement at Ejura, Ghana.

Table 2. Cross-correlation analysis between cassava sap flow density (F_d) and atmospheric factors (R_s and RH). Numbers with bold face are the maximum correlation corresponding to the time lag between the paired variables

Lag time (Minute)	Correlation coefficients	
	R_s versus F_d	RH versus F_d
-120	0.663	-0.700
-110	0.689	-0.701
-100	0.713	-0.700
-90	0.735	-0.697
-80	0.755	-0.693
-70	0.772	-0.688
-60	0.789	-0.681
-50	0.803	-0.673
-40	0.816	-0.664
-30	0.826	-0.652
-20	0.834	-0.638
-10	0.841	-0.622
0	0.846	-0.605
10	0.845	-0.584
20	0.839	-0.560
30	0.832	-0.535
40	0.823	-0.508
50	0.814	-0.480
60	0.801	-0.450
70	0.788	-0.419
80	0.772	-0.386
90	0.754	-0.353
100	0.735	-0.319
110	0.713	-0.285
120	0.690	-0.252

somehow unclear. Values of g_c varied between 0.7 and 2.1 mm s⁻¹ (mean = 1.4 ± 0.5 mm s⁻¹, $n = 8$). Omega, the decoupling factor, also varied from 0.01 to 0.13 (mean = 0.05 ± 0.03) on day-time basis whereas daily Ω varied between 0.02 and 0.06 with mean value of 0.05 ± 0.02.

To closely follow the diurnal behaviour of the E_c , g_c and Ω , Figure 7 showed the diurnal (06:00–20:00 h) course of the three parameters for a typical day (DOY 353). Transpiration increased rapidly following sunrise and attained a maximum of 0.11 mm h⁻¹ between 09:00 and 11:00 h in the mid-morning when R_s was above 200 W m⁻² and VPD was below 1.0 kPa. Plant water use declined gradually thereafter irrespective of the increasing evaporative demand. Highest canopy conductance values, between 08:00 and 09:00 h, decreased rapidly to the low-

est value shortly before 13:00 h in the afternoon, and increased slightly again late afternoon when VPD becomes less than 1.0 kPa. Value of Ω followed a similar pattern to g_c (Figure 7c), decreased from peak value of 0.10 during the morning time to 0.03 in the afternoon. The diurnal average of Ω was 0.05. On daily basis, g_c was linearly related (data not shown) to Ω and the total explained variance equals 93%, while g_a explained 18%. Omega was found to depend more on the ratio g_a/g_c with R^2 of 0.95.

Discussion and conclusions

Total amount of rainfall from the beginning of the dry months (November) and the end of the experiment (24 December 2002), 54 days period, was 52 mm. This amount of rainfall fell far below the potential evaporation (atmospheric water demand) that was estimated at an average of 4.1 mm day⁻¹. The cassava plants were apparently under water shortage during this study. This was also indicated by the declining trend in profile average soil water with lower values still expected during the experiment, which was not covered by the available data (Figure 1). About 21% of the available energy of the net radiation input to the canopy of cassava was used for transpiration, which also met 24% of the atmospheric water demand. Low values of plot-level transpiration observed in this study agreed with previous results (Alves and Setter, 2000; El-sharkawy and Cock, 1984). Cross-correlation analysis revealed an undetectable lag time (at 10 min sampling resolution) between R_s and sap flow whereas xylem flow led humidity by up to 110 min. Perhaps because cassava stem is small and plant is experiencing stress under which the root capacitance is expected to be far greater than the stem capacitance in the flow path above the sensor. Under this drought condition, radiation and VPD explained 83% of the variations in hourly water use ($P < 0.05$, ANOVA). Inspection of Figure 4 combined with the fitted parameter ($b = 267 \text{ W m}^{-2}$), showed that the canopy soon reached light saturation with $R_s < 300 \text{ W m}^{-2}$. Thus, the increase in E_c observed at high values of R_s may not be due to stomatal opening as a result of R_s but may be from an increase in VPD that increased the driving

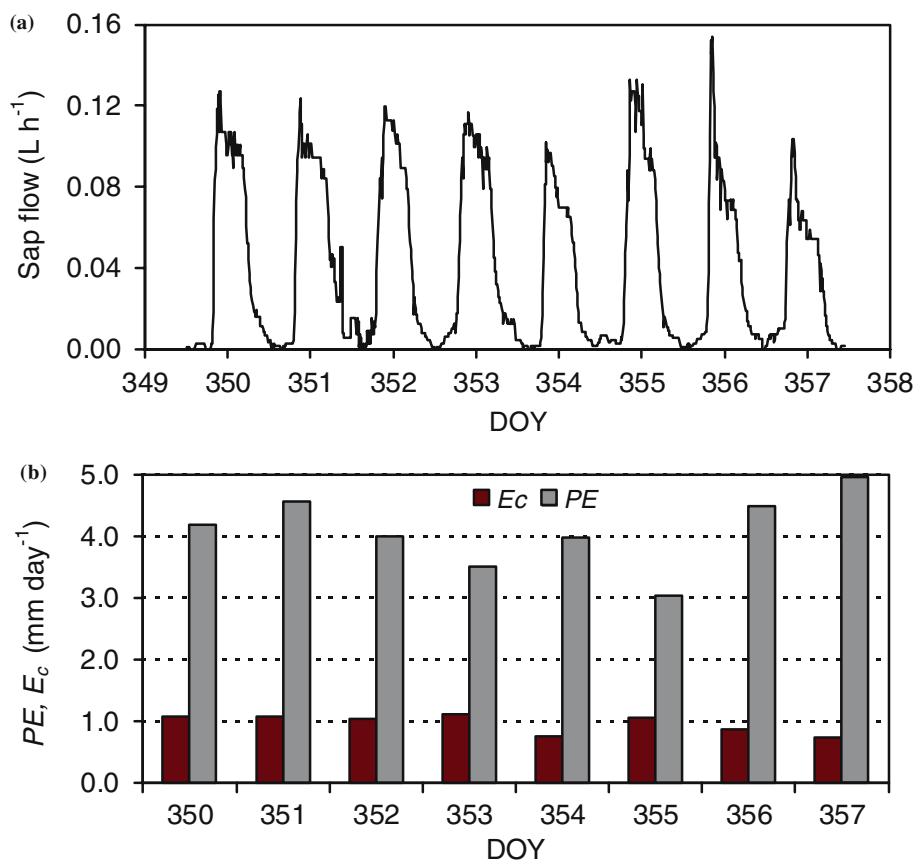


Figure 3. (a) Diurnal pattern of cassava sap flow and (b) daily values of potential evaporation (PE) and plot-level canopy transpiration (E_c) between DOY 350–357, 2002.

force of transpiration especially when VPD is lower than 1.0 kPa (Figure 4a, d). Obviously transpiration increased from sunrise with increasing VPD until a threshold of about 1.0 kPa was reached and further increases in evaporative demand led to a sharp decrease in transpiration. A similar behaviour was reported for potted cassava under well watered and stressed conditions (El-sharkawy and Cock, 1984) and is indicative of stomatal regulation of transpiration.

Daily canopy conductance was estimated at 1.4 mm s^{-1} while the diurnal average was 1.6 mm s^{-1} . Connor and Palta (1981) gave the probable range of maximum conductance encountered in a rainfed environment as $3.0\text{--}5.0 \text{ mm s}^{-1}$ for unstressed cassava while stressed cassava operates at less than 1.0 mm s^{-1} . The discrepancy observed between these two studies results from the scale of measurement which are leaf and whole-plant scales. Comparison of the

leaf conductance to the values presented here would require porometer measurement of a large number of representative sunlit and shaded leaves coupled with accurate determination of LAI (Lu et al., 2003). The TMS30572 variety tested here may be comparable (in response) with a vigorous variety M Mex 59 studied in CIAT, Colombia (Connor and Palta, 1981). The variety studied here was described as having good canopy characteristics, moderately leafy and good harvest index. It is also high yielding with high stay clean ability (O O Aina, IITA, Ibadan: personal communication).

Daytime stomatal response to solar radiation did not show the usual hyperbolic shape common with unstressed plants, but the response to VPD was consistent with expected pattern. The variability in g_c increased significantly as R_s decreased below 300 W m^{-2} and VPD decreased below 1.0 kPa (Figure 5). Maximum diurnal g_c

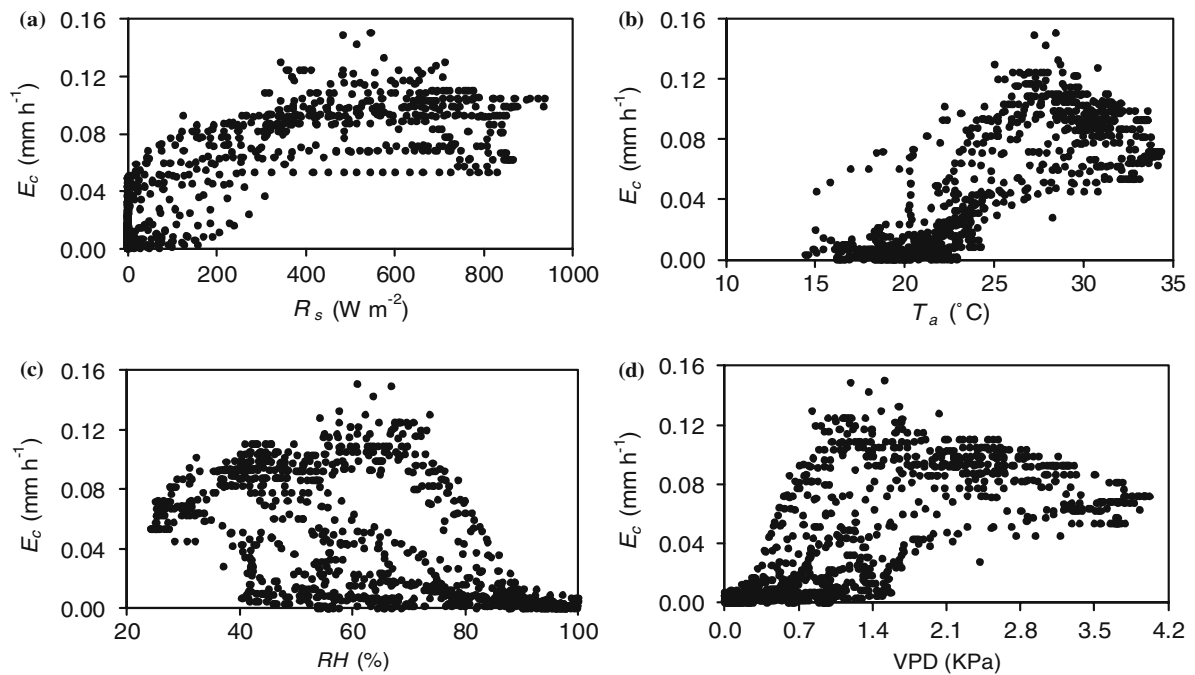


Figure 4. The dependence of cassava transpiration on transient meteorological conditions (a) solar radiation (R_s), (b) air temperature (T_a), (c) relative humidity (RH), and (d) VPD, during DOY 350–357, 2002 at Ejura, Ghana.

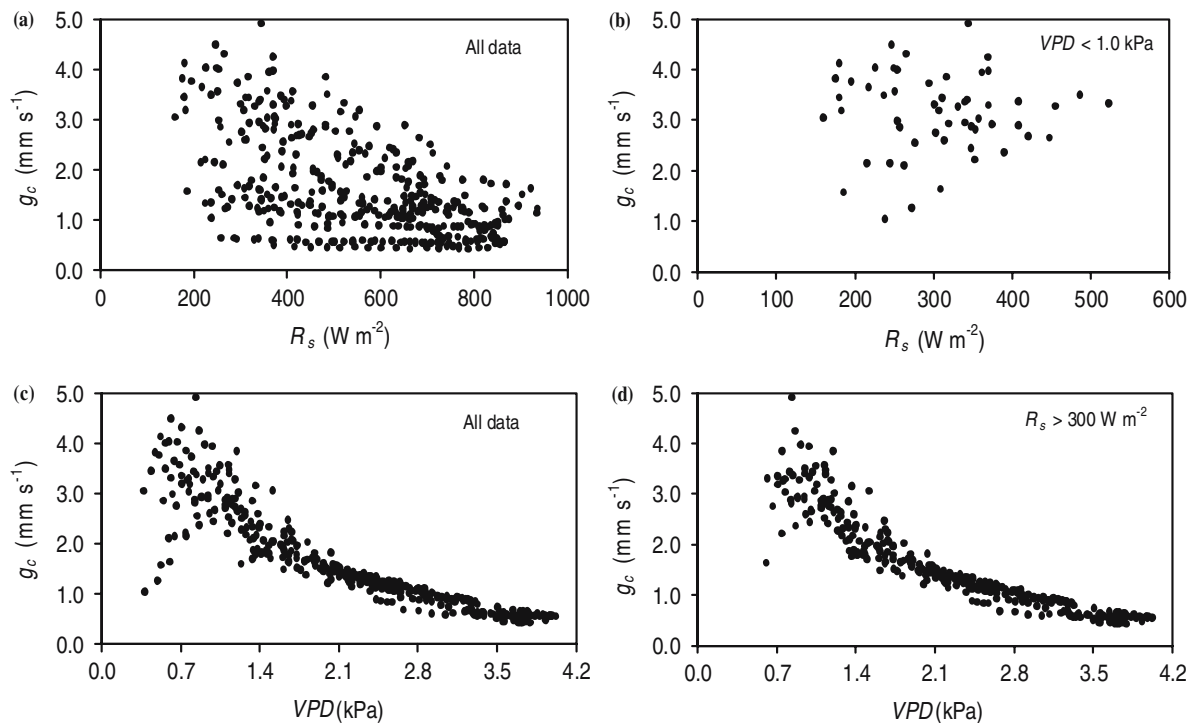


Figure 5. Response of daytime canopy conductance (g_c) to (a) solar radiation (R_s) with all data, (b) solar radiation (R_s) when $VPD < 1.0 \text{ kPa}$, (c) VPD with all data, and (d) VPD when $R_s > 300 \text{ W m}^{-2}$.

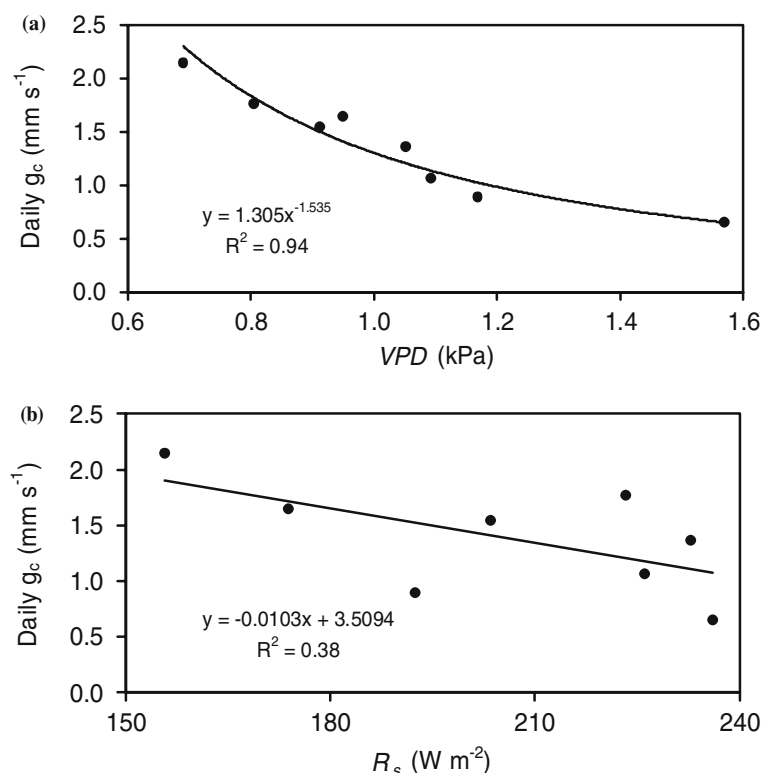


Figure 6. Response of daily canopy conductance (g_c) value of cassava plant to (a) VPD and (b) R_s during DOY 350–357, 2002 at Ejura, Ghana.

was observed in the mid-morning time when the R_s was about 200 W m^{-2} and VPD was less than 1 kPa. As VPD increased from 1.0 to 3.5 kPa, canopy conductance decreased to values around 0.5 mm s^{-1} without the limitation of R_s (Figure 5d). Connor and Palta (1981) found higher correlations, similar to this result, between leaf conductance and leaf-air vapour deficit especially in stressed cassava at non-limiting quantum flux density. The observed decrease in g_c with increasing VPD correspond to a decrease in transpiration, indicating strong stomatal control. In addition, Figure 4d may be re-plotted to show the combined effects of (low or high) wind speed and VPD on transpiration particularly beyond the light saturation value of R_s and at higher VPD ($> 1.5 \text{ kPa}$) as shown in Figure 8. Analysis of wind effects showed that wind has little impact on the cassava water use during this period. When wind speed was less than 2 m s^{-1} (low), decrease in VPD explains 64% of the variation observed in diurnal E_c whereas the % of vari-

ance explained at wind speed $> 2 \text{ m s}^{-1}$ was 61%. This 3% wind effect was insignificant compared to the closure of stomatal aperture to regulate water use in response to increasing VPD. A simple least squares fit relating daily E_c and g_c (Figure 9) showed that conductance explained close to 92% of the observed variance in daily transpiration.

Very low daily and daytime average values of decoupling factor, suggest that transpiration of cassava was mainly controlled by stomata conductance and that cassava canopy was strongly coupled to the atmosphere (Figure 7 b, c). Granier et al. (1996) obtained a value of 0.2 for natural rain forest canopy while Lu et al. (2003) obtained value of 0.25 for grapevine canopy and they concluded that the canopies were strongly coupled with atmosphere. Decoupling factor from 0.1 to 0.2 is generally referred as 'strong' coupling while values between 0.4 and 0.5 are 'moderate'. The average value of 0.05 presented in this study is 'very strong' even though cassava

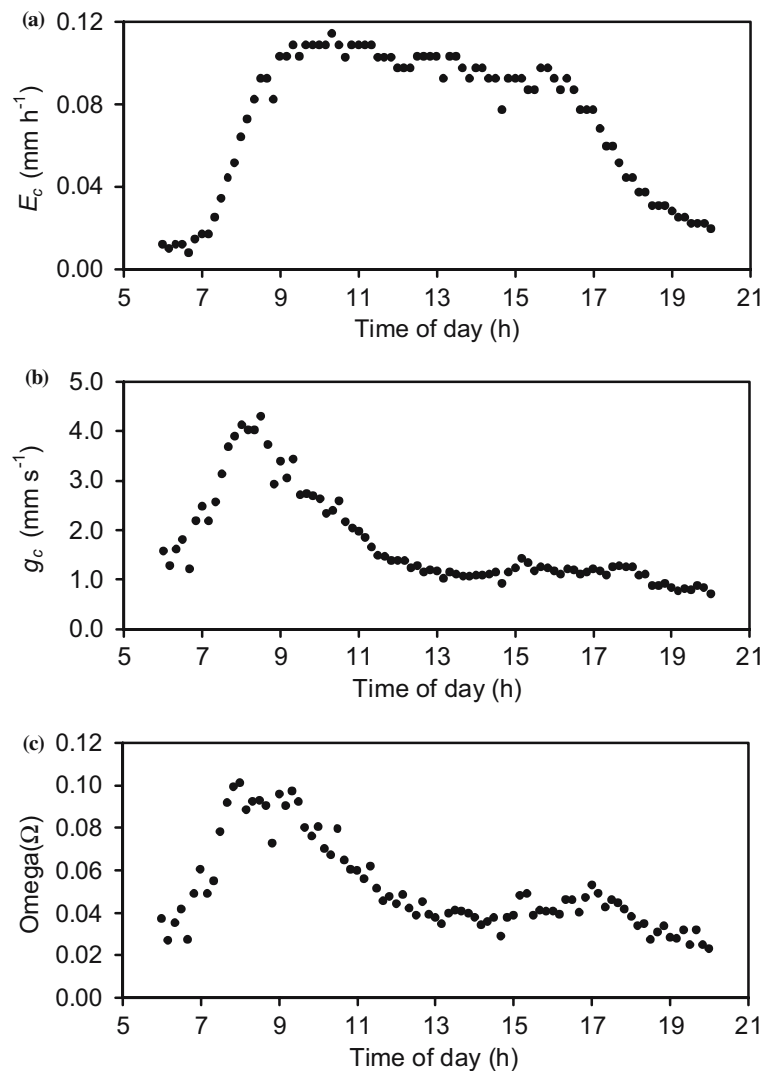


Figure 7. Diurnal pattern of cassava (a) transpiration (E_c), (b) canopy conductance (g_c), and (c) decoupling factor (Ω) for a typical day (DOY 353) in 2002.

has other adaptive mechanisms to respond to water shortage besides stomata closure. This value indicates that a 10% change in g_c will result to more than 9% change in transpiration. Cassava grown under field conditions is known to adapt to water stress conditions through such mechanisms as stomata closure, reduction in leaf area, osmotic adjustment, increasing root length and ultimately shedding of leaves (Alves and Setter, 2000, 2004; Aina et al., 2004; Connor et al., 1981; Connor and Palta, 1981). Unlike the root growth in search of water, which is limited because cassava has sparse root system (Connor

et al., 1981), or leaf loss and osmotic adjustment that involve the sacrifice of growth reserves previously assimilated (yield penalty), stomata closure reduces the current carbon assimilation capacity of plant under stress with a view to increasing the water use efficiency (WUE) to maintain the existing yield and/or increase it (Blum, 1996; Connor and Palta, 1981). Water-stressed cassava was also reported to be capable of leaves movement that tends to (1) maximize light interception, and hence WUE, at times when VPD is low (heliotropic response), and (2) minimize light interception at times when VPD is

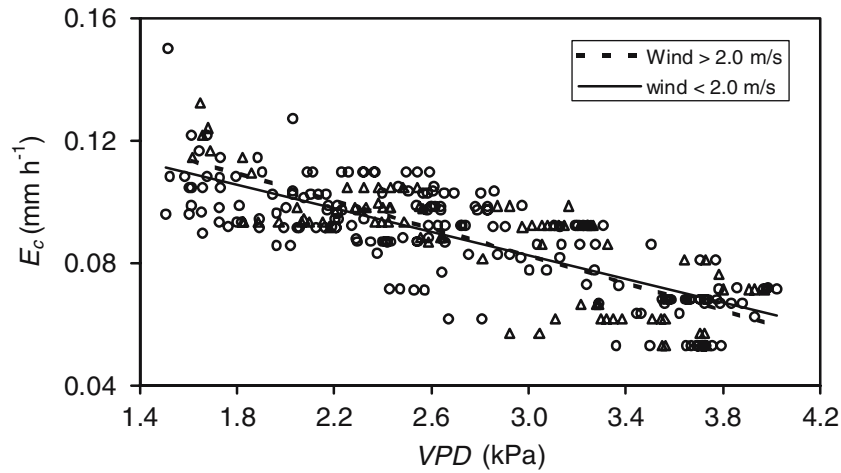


Figure 8. Effect of increasing evaporative demand on cassava water use under low ($< 2.0 \text{ ms}^{-1}$) and high ($> 2.0 \text{ ms}^{-1}$) wind speed and limited soil water at Ejura, Ghana.

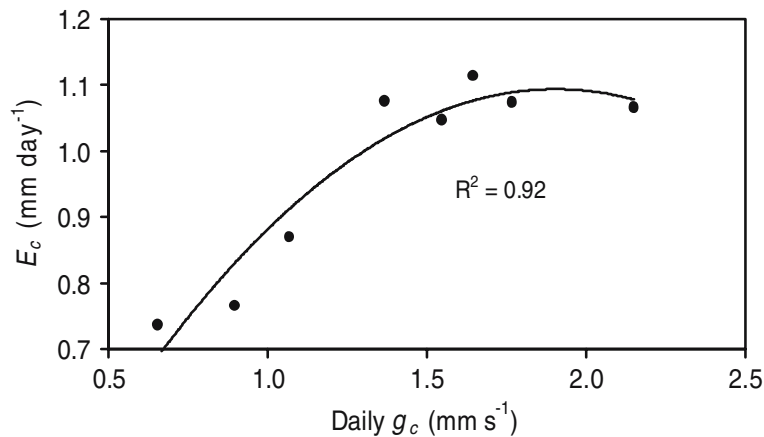


Figure 9. A simple relationship between daily canopy transpiration (E_c) and conductance (g_c) of cassava between DOY 350 and DOY 357, 2002 at Ejura, Ghana.

high (drooping leaf movement) combined with direct stomata control to reduce water loss at time of low WUE (El-sharkawy and Cock, 1984). In all, the stress hormone abscisic acid (ABA) has been fingered as playing a significant role in the regulatory system that contribute to cassava's sensitivity to water deficit (Alves and Setter, 2000).

In conclusion, estimated canopy conductance and its relation to rapid changes in environmental variables provided a good overview of stomatal control of transpiration at the whole-plant

canopy level. Cassava stomatal mechanism tends to maintain stable internal water status under water shortage and increasing evaporative demand. Further studies are required for field-grown cassava under well-watered condition so that the data could be integrated to model the response of g_c to environmental variables. As special sap flow sensors are currently becoming available commercially, monitoring of younger cassava plant of smaller stem sizes would be possible using the relatively simple, cheap and efficient Granier measurement applied in this study.

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