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ARTICLE

Land-use Changes Alter Energy and Water Balances on an African *Brachiaria* Pasture Replacing a Native Savanna in the Orinoco llanos

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ABSTRACT

The seasonal changes in the energy balance after the substitution of a herbaceous savanna by a *Brachiaria* field located in the Orinoco lowlands were assessed over an entire year using the eddy covariance technique. Simultaneously, an herbaceous savanna was monitored as a control. This work provides evidence that the vegetation replacement lead to different patterns of energy and water balance. The seasonal trends of the latent heat flux (λE) to available energy (Ra) ratio tended to decrease as senescence increased due to seasonal influence of air humidity mole fraction deficit and soil water content on leaf area index (LAI) and surface conductance (gs). Therefore, the partitioning of the available energy depended on both climatological (i.e., solar radiation, volumetric soil water content and air humidity mole fraction deficit) and biological variables (i.e., conductance behavior and LAI) which were stress-induced. For the wet season, the seasonally averaged daily λE in the *Brachiaria* field (i.e., 0.8 ± 0.1 mm d^{-1}) was 1.3-fold higher than that in the herbaceous savanna (i.e., 0.6 ± 0.1 mm d^{-1}) (Mann-Whitney U-test). For the dry season, the value was 2.7 ± 0.6 and 2.2 ± 0.4 mm d^{-1}, respectively, these means values were not significantly different. In the *Brachiaria* and herbaceous savanna stands, the annual evapotranspiration was 731 and 594 mm year^{-1}, respectively, and the annual ratio of evapotranspiration to precipitation was 0.52 to 0.42 respectively. In *Brachiaria* field, the deep drainage was relatively lower (43% of total precipitation) than that in the herbaceous savanna stand (53%) leaving a similar amount of water to increase soil storage. The current shift in land cover decrease deep drainage and increased λE by water uptake from a pasture with high belowground phytomass and LAI.

1. Introduction

Savannas are a major component of the world´s vegetation covering one-sixth of the land surface [1] and supporting most grazing lands [2]. In these lands, the major areas dedicated to extensive beef production are the Neotropical and Australasian savannas. The well-drained Neotropical savannas are characterized by a marked seasonal decrease in dry matter accumulation and palatability as the transpiring surfaces are reduced [3]. As a result,

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constraint on livestock production is evident. Therefore, strategies have been developed to improve land management on the basis of replacing 250 x 10^6 ha of native vegetation by drought-resistant African pastures in the last 30 years [4,5,6,7,8]. Specifically, *Brachiaria* is estimated now to cover 20-30 % of South American savannas [9]. The consequences of this extensive replacement have scarcely been documented [10]. However, there is major concern over accelerated land degradation and reduced water availability following inadequate pasture management [11]. The overall aim of this study is to compare the effect of seasonal conditions on the water vapour fluxes of two contrasting surface forcing conditions, as represented by a cultivated *Brachiaria* field and a native savanna side by side under the environment of the Orinoco lowlands. The *Brachiaria* field presents a mat-forming surface and the savanna features an open and erect canopy. This situation might have a disproportionate influence on the surface-forcing condition of the Neotropical plains.

This paper focuses on one dimension of vegetation hydrology: evapotranspiration. To accomplish this task, the micrometeorological approach is suitable [12,13,14,15,16]. Comparing measurements of water flux vapour as a function of contrasting canopy features and environmental conditions revealed the genetic potential and highly successful adaptation of *Brachiaria* to the Neotropical savanna environment.

This study was carried out within the Orinoco basin (1.1 x 10^{12} m^2), which extends from the northern region of South America (10° 56' N; 67° 25'W) to the Orinoco River in the south (7° 46' N; 64° 25' W). In this regional environment, the patchiness of *Brachiaria* fields and herbaceous savannas provides favorable circumstances for undertaking a comparative study of the water vapour fluxes. Specifically, we considered that if seasonal water demand and supply are determinant of vegetation functioning, then replacing savanna forcing conditions by changes in land use should modify water balance. By contrast, if resources such as soil water and holding capacity turned out not to limit forage development, then we could expect other factors to be determinants.

The aims of the present work were to: 1) understand favorable circumstances for undertaking a comparative study of energy and water vapour fluxes between *Brachiaria* field and herbaceous savanna stand in the Orinoco lowlands using the eddy covariance method; 2) evaluate the processes controlling water vapour transfer as generated by different canopy forcing conditions; and 3) compare the water balance as based on the mass curves, Kareliotis` approach, between the *Brachiaria* field and the surrounding herbaceous savanna stand. The described processes and controls might be representative of major Neotropical savannas.

2. Materials and Methods

2.1. Description of the Study-sites and Treatments

At the Experimental Station of Eastern University (9º 45´ N, 63º 27´ W) in Monagas State, Venezuela, a 40-ha plot covered with herbaceous savanna (i.e., savanna with less than 3% of woody cover) was selected. The infertile soil is a sandy loam belonging to the Maturin series, which is within the oxic-paleustults as classified by Espinoza [17] in accordance with the U.S. Taxonomy [18]. The soil infiltration rate ranges from 26 to 36 mm hr^{-1}[19]. The annual mean precipitation is 1014 mm; the growing season spans May to November with 885 mm. The annual mean class A pan evaporation is 2226 mm and the annual mean temperature is 25.9 ºC. Those variables correspond to 38-year mean.

The 40-ha plot was divided into two sub-plots of 20 ha each. A sub-plot was plowed and a field fertilized with 400 kg ha^{-1} of 12-12-17 NPK and *Brachiaria decumbens* (L.) Staff was planted (August, 16th 2000) to monoculture at a density of 2,000 viable seeds per m^2. Because of its dense, rigorous mat-forming surface, the *B. decumbens* formed a sward with a closed canopy throughout the year. The carrying capacity of this stand was 1.0 Animal Unit (AU) ha^{-1}. In the other 20-ha sub-plot, the herbaceous savanna (< 3% tree cover) forms an open canopy dominated by species of the genus *Trachypogon* and *Axonopus* with upright tillers.

Previous to the experimental setup, the *Brachiaria* field and the herbaceous savanna sub-plots were regularly grazed under conditions representative of those under normal use in the Orinoco lowlands. At the beginning of the dry season (2008), before microclimatological measurements, the plots were excluded from grazing.

2.2. Leaf Area Index and Belowground Dry Mass

At each sub-plot, the leaf area index was determined monthly with a plant canopy analyzer (LI-2000, LICOR, Lincoln, Nebraska, USA). Ten 1 m x 1 m soil samples were selected monthly at random and the soil was excavated down to 0.5 m. The below-ground phytomass was separated by the flotation method [20] and oven-dried at 80°C until constant dry mass.

2.3. Measurement Systems

At each sub-plot, energy and water vapour flux densities were measured continuously by the eddy flux covariance

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(EC) method [21,22] using an open path infrared gas analyzer (LI-COR 7500, Lincoln, NE) coupled with a 3D sonic anemometer (Solent A1003R, Gill Instruments, Lymington, UK) at 2 m above the ground for the *Brachiaria* and herbaceous savanna stands. EC was processed every 30 minutes with the EdiRe software (version 1.4.3 1167, R Clement, University of Edinburgh) including despiking, double rotation for deviation of time lag spectral corrections, Webb´s corrections [23] and the atmosphere stability test. Weekly clearing frequency limited the problem of optical contamination to a minimum. Total incoming and outgoing radiation was measured with pyrradiometers (S.R.I.4 Solar Radiation Instruments, CSIRO, Victoria, Australia). Short wave solar radiation (R_s) over the vegetation was measured with two pyranometers (LI-200X, LI-COR, Lincoln, NE and CM3 Kipp and Zonen, Deft, Holland), and the albedo with a pyranometer (CM3 Kipp and Zonen). The net radiation (R_n) (i.e., net all-wavelength radiation balance) over the canopy was determined with two net radiometers (Funk-type, model S.R.I.4 Solar Radiation Instruments and Q-7.1 Campbell Scientific, Logan, UT). Net radiation at the soil surface (R_{no}) was measured with a tube radiometer (TRL/M3, Delta-T Devices, Cambridge, U.K.) and a net pyrradiometer (S.R.I.4 Solar Radiation Instruments, CSIRO, Victoria, Australia). Measurements were recorded every second and averaged every minute on a Datalogger (21X, Campbell Scientific). All times were local times.

Soil heat flux (G) was measured with a network of ten heat flux plates (S.R.I.9 Solar Radiation Instruments) placed 0.08 m below the soil surface. The net storage of energy (ΔS_E) in the soil column above each soil heat flux plate was determined from the temperature profile [24] measured with 24 AWG copper-constantan thermocouples placed at 0.2 m intervals from each soil heat flux plate to the soil surface. Before field measurements, the full instrumentation was inter-compared to check for consistency.

At each sub-plot, all instruments were installed near the center. Height for the measurements of vertical fluxes of H_2O and momentum was maximized by using the model for source area/footprint analysis as outlined in [25] and [26]. The resulting measurement height over the sub-plots was 2.0 m. The cumulative normalized flux was 0.91 for H_2O.

Volumetric soil water content (θ) was measured daily from a depth of 0.45 m in 0.15 m intervals with a time-domain reflectometer (TDR) (6050X1 Trace System, Soil Moisture Equipment, Santa Barbara, CA). At each soil depth, three probes were buried horizontally and readings were taken with a multiplier (6022 Trace System). Water retention curves were established with a pressure apparatus membrane as outlined in Richards [27]. Matric potential ranging from –0.01 to –0.03 MP_a was determined with a porous funnel.

Ancillary meteorological characteristics were recorded above the canopy at the same height as the eddy covariance systems using an automatic weather station (CM6, Campbell Scientific).

Gaps in data were filled by standardized methods [28,29], and the dataset was completed with measured ancillary data describing study sites, vegetation and climate. For the water and energy fluxes, symbols and notations follow Reifsnyder et al [30].

The pathway for H_2O diffusion between canopy and atmosphere was described by surface (g_s) and aerodynamic (g_a) conductances. Canopy-to-air humidity mole fraction difference was estimated as the difference between the saturation humidity mole fraction at the canopy temperature (T_0) [31] and the air humidity mole fraction at the canopy surface. This, in turn, is determined using the latent heat flux equation on the basis of measurements from vapour pressure at the weather station, the latent heat flux (λE) and the aerodynamic conductance.

To assess the effect of volumetric soil water content on the upper limit of the daily latent heat flux (λE) to available energy (R_a) ratio, a ben-cable form of a piece-wise linear model with nonlinear quantile regression[32] was used. The 0.90 to 0.99 quantiles provide estimates near the upper boundary of the percentage of $\lambda E/R_a$ ratio as it varied with θ[33].

2.4. Aerodynamic and Surface Conductance

The pathway of the water vapour diffusion and heat between the atmosphere and the canopy was expressed by the aerodynamic (g_a) and surface (g_s) conductances. Aerodynamic conductance was estimated from the sonic anemometer measurements considering the additional boundary layer conductance to momentum flux and the atmosphere stability [34,35] as:

$$g_a^{-1} = \frac{u}{u_\Psi^2} + \frac{1}{ku_\Psi}\left[\ln\left(\frac{Z_0}{Z_H}\right) + \Psi_H + \Psi_M\right] \tag{1}$$

Where u is the longitudinal wind speed at the reference height, u_* is friction velocity, k is on Karman´s constant, Z_0/Z_H is the proportion of the momentum roughness lengths for momentum (Z_0) and heat (Z_H) transfer [35] and Ψ_H and Ψ_M are the integrated adiabatic correction factors for heat and momentum, respectively [36]. The proportion was taken as 10, a typical figure for a homogeneous canopy [37].

Surface conductance was estimated by the inverse form of the Penman-Monteith equation [38,39] using measurement of latent (λE) and sensible (H) heat fluxes as well as specific humidity deficit (D) in the equation:

$$g_s^{-1} = \left[\frac{\varepsilon+1}{g_a}\right]\left[\frac{\varepsilon A}{(\varepsilon+1)(\lambda E)}\right] + \frac{\rho_a D}{E} \quad (2)$$

Where ε is the rate of change of saturate humidity with temperature, A is the addition of the available energy for the canopy (A_c) and soil (A_s) (i.e., $A = A_c + A_s$), ρ_a is the molar density of air and E is the evaporation rate.

2.5. Conductance and the Omega Factor

The degree of coupling (Omega factor, Ω)[40] between the canopy and the atmosphere was calculated from the estimates of aerodynamic (g_a) and surface (g_s) conductances to examine the relative contribution of radiation and specific humidity deficit on transpiration using the following equation:

$$\Omega^{-1} = 1 + \left[\frac{\gamma}{\Delta+\gamma}\right]\left[\frac{g_a}{g_s}\right] \quad (3)$$

Where Δ is the slope of the saturation vapour pressure as a function of the air temperature and γ is the psychrometric constant.

This factor describes how closely the vapour pressure deficit at the canopy surface is linked to that in the air outside the canopy boundary layer. At the same time, it allows examination of the contribution of radiation and saturation deficit to the transpiration rate[41]. Ω approaches 1 in well-watered and aerodynamically smoth canopies, where transpiration rate is driven by canopy to air saturation deficit. Thus, when $\Omega \approx 1$, LE tends to equilibrium evapotranspiration as described by the Priestley-Taylor equation. When $\Omega \approx 0$, LE is closely coupled to the atmospheric saturation deficit [41].

2.6. Modeling Surface Conductance by Nonlinear Least Square-optimization

For the hourly data of the seasons, the g_s for the surfaces was expressed as a function of the ancillary meteorological measurements (Q_s = solar radiation, T_a = air temperature, D_a = air humidity mole fraction deficit, δθ = volumetric soil water content deficit and $\delta\theta_{max}$ = maximum value of δθ) by nonlinear least-square optimization [38,42,43,]. An environmental variable analysis was performed to decrease the redundancy of the environmental variates. Thus, the variables were subject to a preliminary analysis by using the variance inflaction factor of variables in a multiple regression equation [44]. Collinear variables (i.e., solar radiation and air temperature) were deleted from the variable set. As a result, the best model was $g_s = g_{smax} f_1(Q_s)\ f_2(D_a)\ f_3(\delta\theta)$, where g_{smax} was the maximum measured g_s and the equations

$$f_2(D_a) = 1 - K_3 D_a \quad (4)$$

$$f_3(\delta\theta) = 1 - e^{K4} \quad (5)$$

$$K_4 = K_5(\delta\theta - \delta\theta_{max}) \quad (6)$$

Where g_{smax} (i.e., K_1) and $K_2 - K_5$ were parameters.

2.7. Water Cycle Dynamics

The water cycle dynamic data was analyzed by using the Chow and Kareliotis`approach [45] as based on the mass curves. Thus, the mass balance equation, in which the system component of precipitation (Pc), conceptual water storage (S), measured as temporal changes in the soil volumetric moisture content Ɵ, at deep layer 0.5 m evapotranspiration (λEc) and run off (Rt= cero in our case) are considered as stochastic processes. The water drained below the 0.5 m depth is considered as the differences of the three component stochastic processes (Pc-λEc-S)

3. Results

3.1. Physical Environment

Climatic seasonality was marked by 99.9 % of the total annual precipitation (i.e., 1397.8 mm) falling during the wet season (Figure 1A). During the dry season, the weather was usually stable with 85 days receiving 83% of the clear sky radiation. Maximum daily solar radiation increased from 20.3 MJ m^{-2} day^{-1} in the dry season to 21.1 MJ m^{-2} day^{-1} in the wet season (Figure 2A). On an annual basis, the stands received 5.9 GJ m^{-2} yr^{-1}. Despite receiving equal annual sums of solar radiation, annual R_n was greater over the *Brachiaria* field (3.1 GJ m^{-2} yr^{-1}) than over the herbaceous savanna stand (2.7 GJ m^{-2} yr^{-1}). Daytime averaged hourly temperature ranged from 25.3 to 31.4 ºC in the dry season and from 20.8 to 31.4 ºC in the wet season (Figure 2B). During the wet season, there were days when the daytime and nighttime averaged hourly temperature overlapped from 0.5 to 1.5 °C. Air humidity mole fraction deficit increased during the dry season and reached a maximum of 24.9 mmol mol^{-1} at the end of the season (Figure 1B).

The volumetric soil water content (θ) was integrated across the upper 0.45 m of the soil profile (Fig. 2C). The daily amount of soil water in the *Brachiaria* and herbaceous savanna stands remained different. With the onset of the dry season, vegetation and the atmosphere depleted water from the soil profile and the vegetation cover dried out. Thus, θ in the *Brachiaria* field was below wilting point (WP) (i.e., 0.087 m^3 m^{-3}) from March to April (i.e., 36 days). In contrast, in the herbaceous savanna stand, it was below WP only in April (i.e., four days). As a consequence, the LAI of the *Brachiaria* field and herbaceous savanna stand became reduced with plant senescence to 1.15 ± 0.08 and 0.45 ± 0.06 m^2 m^{-2}, respectively. This LAI of *Brachiaria* was significantly higher than that in herbaceous savanna stand (Mann-Whitney U-test in Sokal and Rohlf [46]. The rapid decrease in vegetation growth was associated with low soil water-holding capacity of the sandy soils and a high air humidity mole fraction deficit (Figure 1B). As the vegetation growth proceeded during the wet season, θ for the *Brachiaria* field and herbaceous savanna stand reached a maximum of 0.327 and 0.339 m^3 m^{-3}, respectively (Figure 2C). During the measuring period, θ in the *Brachiaria* and herbaceous savanna soils was above field capacity (i.e., 0.220 m^3 m^{-3}) on 152 and 194 days, respectively. Distribution of rainfall and θ variability were determinants of the length of the growing season for both stands, which was shorter in this study (185 days) than that (220 days) for the 38-years average in the same area for prevailing conditions.

3.2. Radiation Balance

During the dry season, the seasonal average daily (R_n/R_s) ratio over the *Brachiaria* field was 0.55 ± 0.01, 25 % higher than that in the herbaceous savanna stand (0.44 ± 0.02) (Mann-Whitney U-test). During the wet season, the value for the *Brachiaria* field (0.53 ± 0.02) was not significantly different from that for the herbaceous savanna stand (0.49 ± 0.063) (Mann-Whitney U-test). The difference (Mann-Whitney U-test) during the dry season between outgoing short wave radiation over both stands (-2.4 ± 0.3 MJ m^{-2} d^{-1} for the *Brachiaria* field and -2.0 ± 0.2 MJ m^{-2} d^{-1} for herbaceous savanna) and outgoing long-wave radiation (-39.9 ± 0.6 MJ m^{-2} d^{-1} for *Brachiaria* and -41.9 ± 0.7 MJ m^{-2} d^{-1} for herbaceous savanna stand) as well as during the wet season in outgoing short wave radiation over the stands (-2.5 ± 0.5 MJ m^{-2} d^{-1} for *Brachiaria* field and -2.1 ± 252 0.4 MJ m^{-2} d^{-1} for herbaceous savanna stand) and outgoing long-wave radiation (-37.3 ± 0.7 MJ m^{-2} d^{-1} for *Brachiaria* field and -38.2 ± 0.3 MJ m^{-2} d^{-1} for herbaceous savanna stand) were associated with site factors such as albedo and surface temperature.

3.3 Energy Balance Closure and Seasonal Energy Fluxes

In the *Brachiaria* field and herbaceous savanna stand, the sensible flux (H), latent heat flux (λE) and available energy (i.e., R_a) were determined concurrently and the outcomes compared by regression statistics [47]. For both study-sites, the relationships showed a high significant slope close to unit (i.e., 0.98 and 0.99, respectively) (r^2 = 0.92 and 0.91, respectively) and the mean square error (RMSE) 18 and 19 Wm^{-2}, respectively.

A comparison between the *Brachiaria* field and herbaceous savanna stand in daily evapotranspiration (λE) and the effect of the seasonal conditions are shown in Figure 1A-D. During the dry season, λE over the two contrasting stands was less than 1.3 and 0.8 mm d^{-1}, respectively as soil water decreased. With onset of the wet season, λE at both stands increased day by day until peaking at 3.7 and 3.5 mm d^{-1}, respectively. Annual λE in the *Brachiaria* field was 731 mm and the herbaceous savanna stand was 594 mm.

3.4. Seasonal Partitioning of Available Energy

During the seasons, two typical daily trends of fluxes in the *Brachiaria* field and herbaceous savanna stand are shown in Figure 3A-B. After replacement of the herbaceous savanna, the changes in forcing surface conditions and water availability contribute to the measured differences. On the typical sunny day during the dry season (March, 12th), R_s over the *Brachiaria* field and herbaceous savanna stand increased to a maximum value of 966 Wm^{-2}. As a result of canopy senescence and decreased LAI, the ratio of R_n above to R_n below the canopy in both stands reached 0.33 ± 0.21 and 0.25 ± 0.16, respectively. These values were not significantly different (Mann-Whitney U-test). The energy flux density of H and λE showed a sinusoidal trend; however, λE presented lower value than H from late morning to afternoon hours. During the midday hours, the H/R_n ratio over both stands reached 0.58 and 0.82, respectively. Bowen ratio (β) over the stands reached a maximum of 2.7 and 8.9, respectively. On a typical day during the wet season (October, 10th), the maximum R_s was 828 Wm^{-2}. The *Brachiaria* field and herbaceous savanna stand canopies heated and the Bowen ratio was positive for most daytime with figures related to site conditions. As λE increased over both sites, β reached values of 0.2 and 0.4, respectively.

On the days during the dry and wet seasons hourly soil storage flux (ΔS_H) in the *Brachiaria* and herbaceous savanna stands (Fig. 3A-B) are a major component of R_n, but decreased during the afternoon hours. Around noon of the day during the dry season, the average daytime convective-to-conductive heat-sharing fraction (ΔS_H/R_n) ratio ranged from 0.18 to 0.80 in the *Brachiaria* field and from 0.10 to 0.60 in the herbaceous savanna stand. On the day during the wet season, the ΔS_H/R_n ratio spanned from 0.07 to 0.60 and from 0.02 to 0.70, respectively. These results indicated that soil

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constituted a differential sink/source of heat.

In the *Brachiaria* and herbaceous savanna stands, the difference between the canopy and the air in temperature (Fig. 3E-F) reached up to 1.3 and 0.6 °C, respectively. On the day during the dry season, the canopy-to-air humidity mole fraction difference (D_c) rose through the morning hours from 1.9 and 1.4 mmol mol^{-1} at predawn respectively, to 47 and 50 mmol mol^{-1} at 12:00 and 14:00 hours, respectively. The variations of the fluxes indicate that λE was affected by both D_a and R_n. For both stands, the multiple regression of λE as a function of R_s and D_a was significantly fitted. In the case of the *Brachiaria* field, the expression was $\lambda E = 21.21 + 0.66\ R_s + 1.40\ D_a$, $p < 0.0001$ for the dry season. In the herbaceous savanna stand, the expression was $\lambda E = 14.51 + 0.01\ R_s + 0.44\ D_a$, $p < 0.0097$ for the dry season. Around noon, during the dry season, g_s in the *Brachiaria* field rose to reach its peak (i.e., 0.6 mol $m^{-2}\ s^{-1}$) in the very early morning hours. Thereafter, it decreased rapidly to reach its lowest value during the rest of the day. For both stands, the multiple regression of λE as a function of solar radiation and air humidity mole fraction deficit was significantly fitted. Thus, in *Brachiaria* field, the relationship was $\lambda E = 27.2 + 0.06\ R_s + 1.75\ D_a$, $p < 0.0001$ for the wet season. In the herbaceous savanna stand, the expression was $\lambda E = -5.77 + 0.24\ R_s + 2.12\ D_a$, $p < 0.0001$ for the wet season. Surface conductance in the stands remained at low values (< 1.0 mol $m^{-2}\ s^{-1}$). On the day during the wet season, g_s over the *Brachiaria* field increased in the daytime rising to a plateau (1.19 ± 0.40 mol $m^{-2}\ s^{-1}$) between 7:00 and 15:00 hours. Thereafter, it decreased to low values during the nighttime. Over the herbaceous savanna stand, the course was different. In this stand, g_s increased to i.e., 0.9 – 1.9 mol $m^{-2}\ s^{-1}$ during the very early morning hours. Thereafter, it decreased and reach values close to zero during mid-day hours. The trend of the surface conductance was associated with canopy-to-air mole fraction difference. On the day during the wet season, $g_s$over both stands increased with R_s and decreased with canopy-to-air humidity mole difference (D_a) (Fig. 3A-F). The trends of wind speed and aerodynamic conductance (g_a) (Fig. 3C-D) were relatively lower in the day during the wet season as compared to that in the day during the dry season. The magnitude of g_a (Fig. 3C-D) was always higher than that of g_s, except for the morning hours of the wet season.

3.5. Proportion of Daily Available Energy (R_a) Used for Evapotranspiration as a Function of Volumetric Soil Water Content, Leaf Area Index and Surface Conductance

The response of evapotranspiration in the *Brachiaria* field and herbaceous savanna stand to θ was quantified by using the daily latent heat flux-to-available-energy ratio (Fig. 4) as originally outlined in Denmead and Shaw [48]. Maximum daily $\lambda E/R_a$ ratio was represented by using a 99Th quantile piece-wise linear regression. The results indicate that upper boundary of the *Brachiaria* field envelope was higher than that for the herbaceous savanna. The regression analysis identified the breakpoint (i.e., the critical θ at which maximum daily $\lambda E/R_a$ is attached) in the interval 0.110 ± 0.022 $m^3\ m^{-3}$ and 0.105 ± 0.021 $m^3\ m^{-3}$, respectively. The equation for the quantifying the upper bound on $\lambda E/R_a$ ratio between minimum and critical θ was daily $\lambda E/R_a = 13.480\ \theta - 0.621$ for the *Brachiaria* field and daily $\lambda E/R_a = 19.989\ \theta - 1.401$ for the herbaceous savanna stand. Therefore, the *Brachiaria* field transpired at a faster rate, despite lower θ.

In the *Brachiaria* and herbaceous savanna stands, the seasonal trend of the ratio $\lambda E/R_a$ was explained by the difference in LAI development (Fig. 5). Seasonal variations in LAI were coupled with changes in moisture availability. Maximum LAI for the *Brachiaria* was (i.e., 2.4 ± 0.2 $m^2\ m^{-2}$) higher than that (i.e., 2.1 ± 0.2 $m^2\ m^{-2}$) for the herbaceous savanna stand. These results indicated that $\lambda E/R_a$ was depressed at low θ because LAI decreased with θ.

Measuring hourly g_s ranges permitted assessing how variation in maximum hourly g_s affected the daily $\lambda E/R_a$ ratio. For both stands, data were fitted by a logarithmic relationship (Fig. 6). In *Brachiaria* field the ratio was less affected as maximum hourly g_s increased from 0.4 to 4.0 mol $m^{-2}\ s^{-1}$. Below 0.4 mol $m^{-2}\ s^{-1}$ (i.e., the critical conductance) the ratio experienced a sharp reduction as a function of the maximum hourly g_s. In the herbaceous savanna stand the ratio was slightly affected from 0.4 to 1.2 mol $m^{-2}\ s^{-1}$, and the critical ratio was similar to that in *Brachiaria* field. However, there was a clear difference between stands in canopy roughness and physiological behavior, and these factors influenced energy exchange and partitioning.

3.6 Modeled Surface Conductance Versus Environmental Variables

The modeled surface conductance as a function of environmental variables indicated that the seasonal trend of g_s showed the influence of the air humidity mole fraction deficit (D_a) and soil water content deficit (δθ). The model accounts for 68 % and 70% of the variance of g_s over the *Brachiaria* field and herbaceous savanna stand, respectively, as a function of maximum g_s, D_a and δθ (Table 1). Comparison of the parameters of the surface conductance model for the *Brachiaria* field and herbaceous savanna stand as determined by nonlinear square optimization in-

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dicates that in the *Brachiaria* field, response of g_s to the changes in the volumetric soil water content deficit was higher than that in the herbaceous savanna stand.

3.7 Water Cycle Dynamics

The seasonal trends of cumulative precipitation and evapotranspiration (i.e., Pc and λEc, respectively) and soil water storage (S) in the 0.0-0.5 m depth for the *Brachiaria* field and herbaceous savanna stand are shown in Figure 7. λEc, in the *Brachiaria* field (731 mm year^{-1}) was higher than herbaceous savanna stand (594 mm year^{-1}), respectively. Soil water storage and water drained below 0.5 m soil layer was lower in *Brachiaria* field (122 mm year^{-1} and 53.1 mm year^{-1}) than herbaceous savanna stand (135 mm year^{-1} and 63 mm year^{-1}), respectively.

4. Discussion

In this analysis, the effect of land-use changes from neotropical herbaceous savannas to cultivated paleotropical grass was evident on roughness-forcing conditions and energy partitioning. The seasonal dynamic of λE could be mainly attributed to the trend of atmospheric demand and water supply for vegetation development. Thus, temporal trends in demand (i.e., energy availability) and supply (i.e., soil water content and leaf-area index) were associated with this tendency.

4.1. Weather and Climate

Seasonal difference between the *Brachiaria* field and herbaceous savanna stand in R_n was due to albedo and surface heating (i.e., difference from incoming to outgoing long wave radiation). In the dry season, the seasonally averaged daily albedo in the stands was 0.15 ± 0.01 and 0.12 ± 0.02, respectively. The divergence between stands in dry seasonally averaged daytime albedo was significantly different (Mann-Whitney U-test). In the wet season, the value was 0.16 ± 0.01 for the *Brachiaria* field and 0.14 ± 0.03, for the herbaceous savanna stand. The deviation between stands in wet seasonally average daytime albedo was not significantly different (Mann-Whitney U-test). The seasonally averaged daily surface heating in the *Brachiaria* field and herbaceous savanna stand was -5.31 ± 0.25 and -7.39 ± 0.30 MJ m^{-2} d^{-1}, respectively, for the dry season and -4.79 ± 0.20 and -5.9 ± 0.20 MJ m^{-2} d^{-1}, respectively for the wet season. The difference between stands in the seasonally averaged daily surface heating was different significantly (Mann-Whitney U-test) for the dry and wet seasons, respectively. In the Orinoco lowlands, the contrast between the two key exotic grasses (i.e., *Brachiaria* as reported here) and *Andropogon* field (as outlined in San José et al [3]) and the herbaceous savanna stand in albedo and surface heating values might lead to differences in mesoscale circulation and cloud convection as described by Keenan et al [49]. There is also evidence of a feedback mechanism between land use change and shifts in resultant climate. That is decline in rainfall over cleared and cropped landscape in Western Australia [50]. In the case of burned and unburned savannas in northern Australia, Beringer et al [51] have found that the consequent contrasting albedo and heating values may significantly modify precipitation patterns.

During the dry season, the mat-forming surface of *Brachiaria* field with high albedo absorbed less energy than that in the upright canopy savanna, where the canopy temperature was consequently higher. The difference in seasonal albedo was associated with the changes in LAI. Similar results have been reported for the African tall grass *Andropogon* field and herbaceous savanna stand of the Orinoco lowlands [3].

4.2 Evapotranspiration and Sensible Heat. Water Cycle Dynamic

The seasonally averaged daily H flux was the main source of the available energy (R_a) in the *Brachiaria* field (7.036 ± 1.186 MJ m^{-2} d^{-1}) and herbaceous savanna stand (4.843 ± 1.008 MJ m^{-2} d^{-1}) during the dry season and it was relatively higher in the *Brachiaria* field (Mann-Whitney U-test). By contrast, λE over both stands was the main component of the available energy during the wet season. However, seasonally averaged daily latent heat flux (λE) for the *Brachiaria* field (6.183 ± 1.427) was not significant different from that for the herbaceous savanna stand (5.609 ± 1.206 MJ m^{-2} day^{-1}) (Mann-Whitney U-test). The results indicate that during the dry and wet seasons, the monthly averaged daily evapotranspiration rate in the *Brachiaria* field (i.e., 0.8 ± 0.1 and 2.7 ± 0.6 mm day^{-1}, respectively) was 1.3- and 1.2-fold higher than those measured in the herbaceous savanna stand (i.e., 0.6 ± 0.2 and 2.2 ± 0.2 mm day^{-1}, respectively) (Mann-Whitney U-test). In the climate seasonality marked conditions by 0.1% of total precipitation occurring during the dry season, the monthly averaged daily λE in the stands was lower than that measured over the Brazilian campo sujo, campo cerrado and campo denso (i.e., 1.1 – 2.5 mm day^{-1}) [52,53,54,55,56]. By contrast, the monthly averaged daily λE during the wet season was similar for the studied stands (2.2 – 2.7 mm day^{-1}) and Brazilian cerrados (i.e., 2.2 – 3.7 mm day^{-1}) [57] with similar precipitation events.

For the *Brachiaria* field and herbaceous savanna stand, the annual evapotranspiration was 731 and 594 mm year^{-1}, respectively (Fig. 7). λE for both stands was similar

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to that reported for a tall grass *Andropogon* field and a herbaceous savanna (721 and 538 mm yr^{-1}, respectively) occurring under similar environmental conditions [3]. By contrast, in the Brazilian cerrado denso and cerrado, the mean annual λE was 823 and 689 mm yr^{-1}, respectively [56]. For *Eucalyptus* open-forest savannas in northern Australia, λE was 870 mm yr^{-1}[58]. These differential responses could be related to woody cover density such as has been reported by Bucci et al [59] for a transpiration gradient along a tree increment in the cerrado and cerrado denso.

For the *Brachiaria* and herbaceous savanna stands, the annual ratio of evapotranspiration to precipitation was 0.52 and 0.42, respectively. This ratio for the *Brachiaria* field was similar to that reported for *Andropogon* field (0.49); whereas the herbaceous savanna stand ratio was lower than those in other herbaceous savannas (0.65) growing in the Orinoco lowlands which featured 1066 mm of precipitation [3] ; and lower also than in the annual grasslands (0.54-0.58) in Ione, California with 559 mm of precipitation [60].

During the dry season, evapotranspiration of the stands proceeded according to the soil water storage levels (Fig. 7). When the rainfall period began, evaporation rose markedly and water drained from the upper (0.50 m) soil layers to layer soil > 0.5 m depth (i.e., Pc - λEc - S). In the *Brachiaria* field, 52 % of the precipitation returned to the atmosphere via evapotranspiration and a smaller amount of water entered soil storage as compared to the herbaceous savanna stand. In both stands, water storage increased from the beginning of the wet season until the middle of the season and λE depended on both precipitation and soil water storage.

The water drained below 0.5 m layer in *Brachiaria* field was relatively lower (43 % of total precipitation) than that in the herbaceous savanna stand (53 %). In the *Andropogon* field, the value was 42% [3]. As consequence, the available water for human consumption, industrial activities and food production was reduced in the exotic grass species by 16-17 %.

These results indicate that after savanna was replaced by *Brachiaria* field the regulation of λE by community functional features (i.e., surface conductance, LAI and root system), phenology and water supply determined a different water balance. Thus, water loss by evaporation in the replaced herbaceous savanna was increased 1.2-fold. In the case of *Andropogon* the value was 1.3 fold [3]. By contrast, after a native oak woodland was replaced by grasslands [61] evapotranspiration dropped from 513 to 378 mm yr^{-1} (i.e., 26 %). In the cultivated Sahel, the fallow replaced by millet crops led to a water loss of 343 to 237 mm yr^{-1} (i.e., 30 %) [62]. Similarly the hydrological cycle of the cerrado savannas of central Brazil was modified as native woody vegetation was replaced by exotic grasses and agricultural crops [55]. The comparative differences might be related to tree density.

4.3 Processes and Controls

The partitioning of the available energy into λE and H, and the resulting effect on boundary layer processes depended on both biotic and abiotic factors. The relative control of the climatological variables was elucidated from volumetric soil water content and air humidity mole fraction deficit. The biological responses were adequately estimated by conductance behavior and leaf area index. As the dry season proceeded, the evaporation fraction of the available energy tended to decrease with increasing senescence due to the seasonal influence of control effects such as air humidity mole fraction deficit, and soil water content on leaf area index and surface conductance.

The annual variations in the daily $\lambda E/R_a$ ratio at each stand were in phase with variation in soil moisture content, LAI and surface conductance (Fig. 4-6). When the ratio was expressed as a function of θ, the upper bound of the envelope for the *Brachiaria* field (0.87) was greater than that for the herbaceous savanna stand (0.80). In the case of the herbaceous savanna stand, the seasonal averaged ratio for the wet season (0.68 ± 0.10) was similar as that reported for a tree and scrub woodland cerrados, accounting for 0.60 during the wet season [52]. In the *Brachiaria* field and herbaceous savanna stand, a sharp decrease in the ratio occurred below the critical soil water content (θ_c) at both stands (i.e., 0.111 ± 0.022 and 0.107 ± 0.021 m^3 m^{-3}, respectively). Thus, the *Brachiaria* field was more tolerant of low soil water potential than that in the herbaceous savanna stand. Similar results for *Brachiaria* have been reported by Mattos et al. [63]. The difference between stands in the response of the $\lambda E/R_a$ ratio as a function of θ was related to the total below-ground dry mass as *Brachiaria* partitioned a larger value (720 ± 65 gm^{-2}) than that in the herbaceous savanna stand (379 ± 48 gm^{-2}) (Mann-Whitney U-test). Therefore, the *Brachiaria* seems to withstand water-stressed conditions on the basis of an extensive root system exploring large soil volume over a long period. Furthermore, the root system of *Brachiaria decumbens* features height hydraulic conductivity under conditions of high evapotranspiration and water stress [63,64]. These traits are likely to delay the onset of the dry season.

Over the *Brachiaria* field and herbaceous savanna stand, the average daily $\lambda E/R_a$ ratio was 0.23 ± 0.04 and 0.21 ± 0.03, respectively, during the dry season, and 0.66 ± 0.10 and 0.68 ± 0.09, respectively, during the wet

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season. Similar seasonal ratios have been reported for intensively farmed land in the paleotropical savannas of Eastern Burkina Faso [65]. In this location, the $\lambda E/R_a$ ratio was 0.23 in the dry season and 0.71 in the wet season. This similarity between the Neotropical and Paleotropical sites in seasonal ratios might be related to a comparable development of the leaf area index. Here, monthly averaged daily $\lambda E/R_a$ ratio for both stands increased similarly as LAI does (Fig. 5). Thus, LAI development explained the seasonal changes of the ratio across the pasture-savanna mosaic. As θ directly affected the $\lambda E/R_a$ ratio more strongly when the soil was markedly dry. The difference between stands in the linear relationship of $\lambda E/Ra$ on LAI was not significant when the test of heterogeneity between the slopes was carried out [46].

For the *Brachiaria* field and herbaceous savanna stand, the daily $\lambda E/R_a$ ratio was logarithmically related to maximum hourly g_s (Fig. 6). Similarly, the logarithmic increase of $\lambda E/R_a$ with increase in maximum hourly g_s has also been reported for a savanna woodland continuum [3]. The short-closed canopy of *Brachiaria* with maximum hourly g_s exceeding the critical value 0.8 mol m^{-2} s^{-1} was less-coupled to the atmosphere as compared with the open tall savanna when the daytime averaged hourly Omega (Ω) was 0.21 ± 0.15 and 0.12 ± 0.05, respectively, for the wet season. These values were significantly different (Mann-Whitney U-test). In the herbaceous savanna stand, the reduction in maximum hourly g_s of less than the critical value 0.4 mol m^{-2} s^{-1} was related to a sharp decrease in the ratio. In a tree and scrub woodland cerrado, similar critical values of g_s (0.4-0.5 mol m^{-2} s^{-1}) were reported during most of the daytime hours [52].This measured low critical g_s in the herbaceous savannas might be acting as a water limiting mechanism. Here the silica body deposited around the stomatal apparatus in the native grasses [66] might contribute to decreased stomatal aperture. Low critical g_s in native grasses have been reported by Baruch et al. [67]. They reported that at a leaf-air vapour pressure difference less than 1 KPa, g_s was 40% lower in the native grasses from the Orinoco lowlands than that in the exotic grasses from the Paleotropical savannas.

The modeled surface conductance was a function of the air humidity mole fraction deficit (D_a) and volumetric soil water content (θ). Similar explanatory factors have been reported for other Neotropical, Paleotropical and Australian savannas [3,13,14,39,65,68,69,70]. Specifically, in *B. decumbens*, Mattos et al. [63] have found that stomatal conductance varied directly with the volumetric soil water content. Whitley et al. [71] compared the parameter values of a modified Jarvis-Stewart model applied across five contrasting Australian woodlands and forests. Similarly to the Orinoco stands, they stressed the relative effects of the vapour pressure deficit and soil moisture on canopy water flux.

5. Conclusions

In this study, evidence is provided showing that replacement of the native herbaceous vegetation by a *Brachiaria* field led to different patterns of energy and water balance. Large expanses of savanna have been transformed into *Brachiaria* fields. Therefore, the future pasture-dominated ecosystem could come to occupy large areas of the savannas. We found that the current shift in land cover decreases soil water storage from 740 to 612 mm and increases λE because of more water uptake by the pasture due to *Brachiaria*'s denser root system and higher LAI. Considering that the Orinoco lowland vegetation is an herbaceous savanna-woodland continuum, the hydrological effect of savanna conversion seems to depend upon tree density. Thus, the renewal of herbaceous savanna by a *Brachiaria* and *Andropogon* fields [3] contribute to an evapotranspiration increase of 1.23 and 1.31 fold-times, respectively. These conditions might affect 10% of the Orinoco lowlands [72], whereas, the replacement of a savanna woodland by the African *Brachiaria* and *Andropogon*[3] lead to an evapotranspiration decrease of 1.0 – 1.5%. Understanding water use efficiency of these vegetations could be important for delineating environmental changes and energy balance on the regional scale. Furthermore, these variations could have a modifying feedback on the climate [73,74,75,76] and water budget [77]. In contrast, models elaborated by Hoffmann and Jackson [78] indicate that precipitation and evapotranspiration could be reduced by 10 % and 6%, respectively, whereas temperature could increase by 0.5°C, as could the frequency of dry periods. They have speculated that the regional conversion could increase deep soil water storage and reduce λE because of less water uptake by deep roots, especially during the dry season. As a consequence, in this scenario, the climate could become drier. In the particular case of the replacement of a herbaceous savanna by a grassfield, the relative response appears to depend upon the disturbance conditions of the displaced savanna.

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Supplement

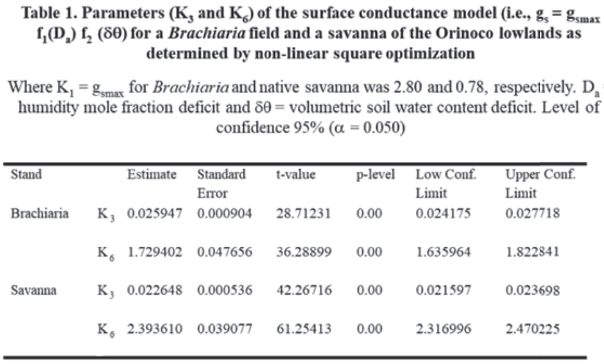

Table 1. Parameters (K_3 and K_6) of the surface conductance model (i.e., $g_s = g_{smax} f_1(D_a) f_2(\delta\theta)$ for a *Brachiaria* field and a savanna of the Orinoco lowlands as determined by non-linear square optimization

Where $K_1 = g_{smax}$ for *Brachiaria* and native savanna was 2.80 and 0.78, respectively. D_a = humidity mole fraction deficit and $\delta\theta$ = volumetric soil water content deficit. Level of confidence 95% ($\alpha = 0.050$)

Stand		Estimate	Standard Error	t-value	p-level	Low Conf. Limit	Upper Conf. Limit
Brachiaria	K_3	0.025947	0.000904	28.71231	0.00	0.024175	0.027718
	K_6	1.729402	0.047656	36.28899	0.00	1.635964	1.822841
Savanna	K_3	0.022648	0.000536	42.26716	0.00	0.021597	0.023698
	K_6	2.393610	0.039077	61.25413	0.00	2.316996	2.470225

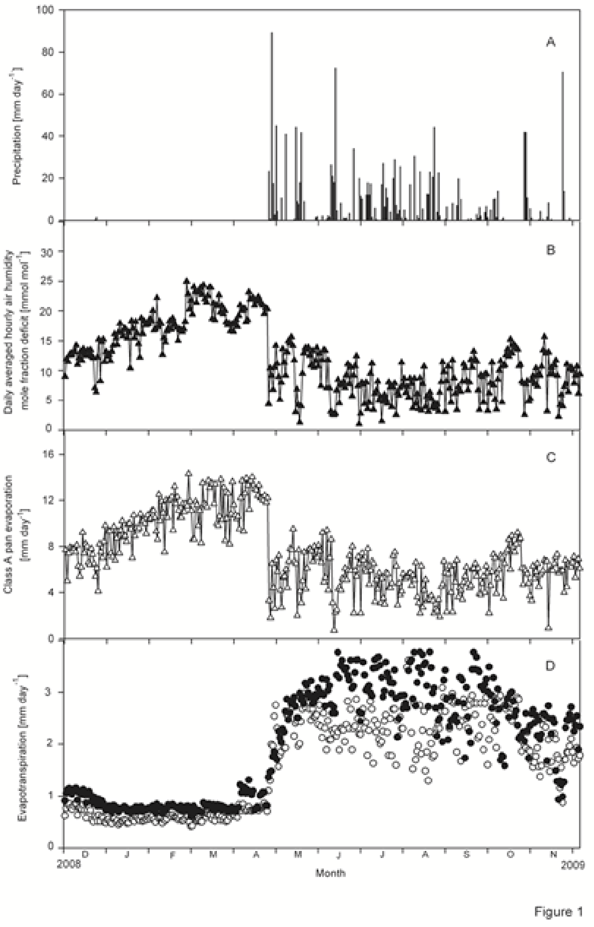

Figure 1. (A) Precipitation, (B) Daily averaged hourly air humidity mole fraction deficit, (C) Class A pan evaporation and (D) Evapotranspiration in a *Brachiaria* field (●) and a herbaceous savanna (○) of the Orinoco Lowlands.

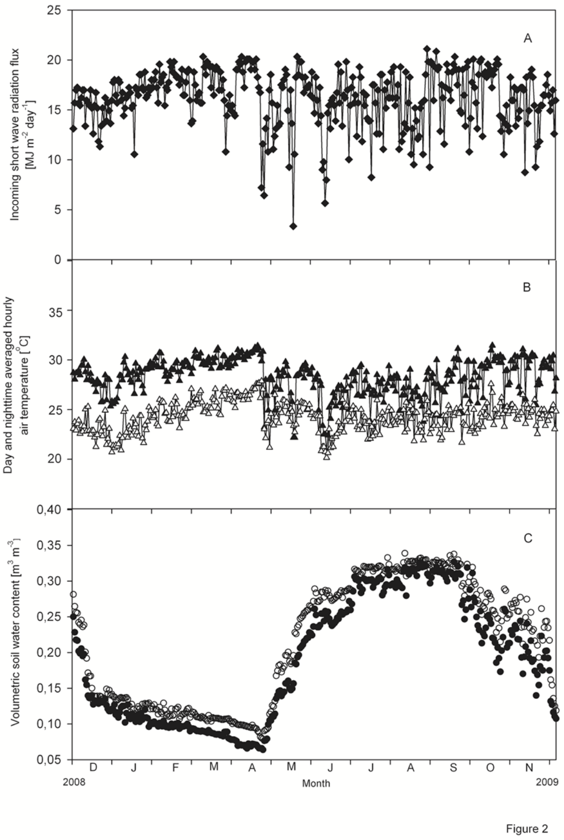

Figure 2. (A) Incoming short wave radiation flux, (B) Day (▲) and nighttime (△) averaged hourly air temperature, and (C) Volumetric soil water content in a *Brachiaria* field (●) and a herbaceous savanna (○) of the Orinoco lowlands.

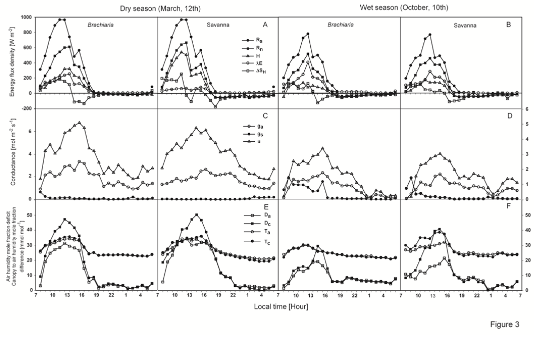

Figure 3. (A-B) Hourly values of energy budget components in a vegetational mosaic of the Orinoco lowlands. R_S = incoming short wave radiation; R_n = net radiation; H = sensible heat flux; λE= latent heat flux; ΔS_H = soil net storage heat flux. (C-D) Aerodynamic (g_a) and surface (g_s) conductances, and wind velocity (u). (E-F) Air humidity mole fraction deficit (D_a), canopy-to-air humidity mole fraction difference (D_c), air temperature (T_a) and canopy temperature (T_c). Measurements taken over a *Brachiaria* field and a herbaceous savanna in typical days during the dry and wet seasons of the Orinoco lowlands.

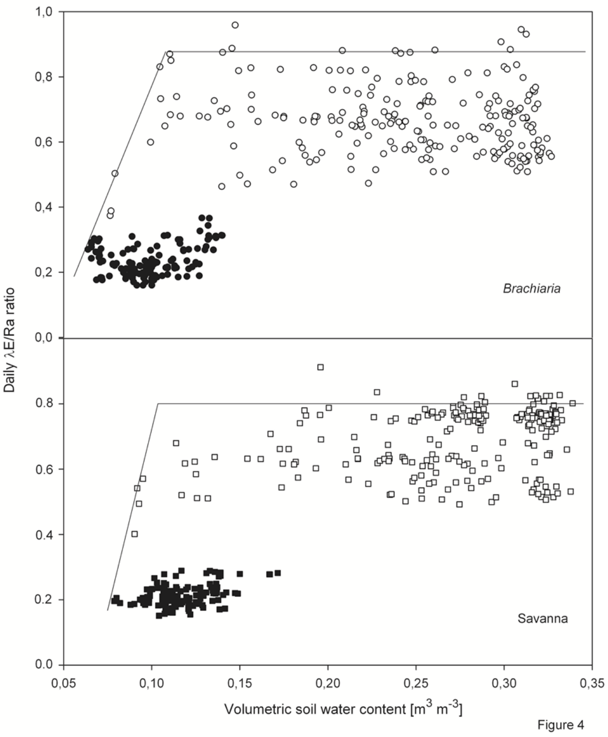

Figure 4. Daily latent heat flux to available energy ratio ($\lambda E/R_a$) as a function of volumetric soil water content (θ) in a *Brachiaria* field (A) and a herbaceous savanna (B) for the dry (●) and wet (○) seasons of the Orinoco lowlands. Maximum daily $\lambda E/R_a$ ratio is represented by using a 99th quantile piece-wise linear regression.

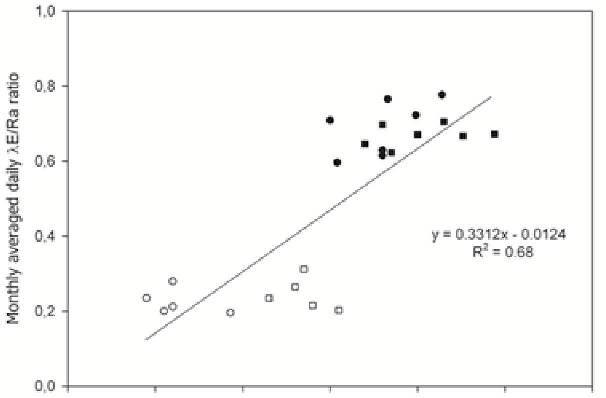

Figure 5. Monthly averaged diurnal latent heat flux to available energy ratio (λE/Ra) as a function of leaf area index (LAI) in a *Brachiaria* field (□ dry season; ■ wet season) and a herbaceous savanna (○ dry season; ● wet season) of the Orinoco lowlands.

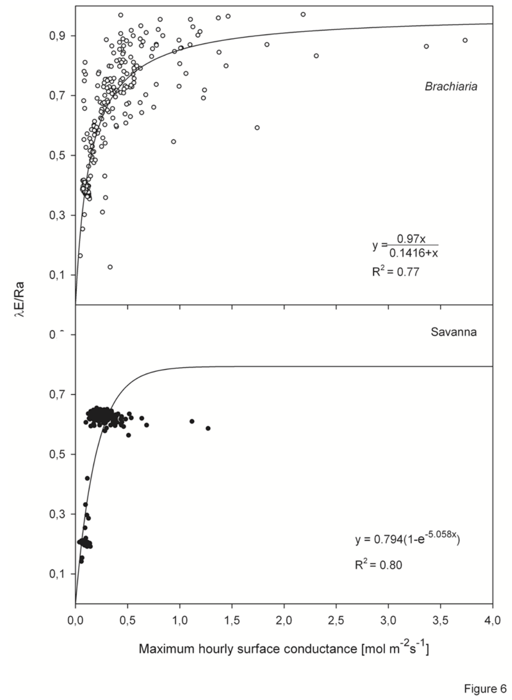

Figure 6. Daily latent heat flux to available energy ratio (λE/Ra) as a function of maximum hourly surface conductance (gs) in a *Brachiaria* field (A) and a herbaceous savanna (B) of the Orinoco lowlands.

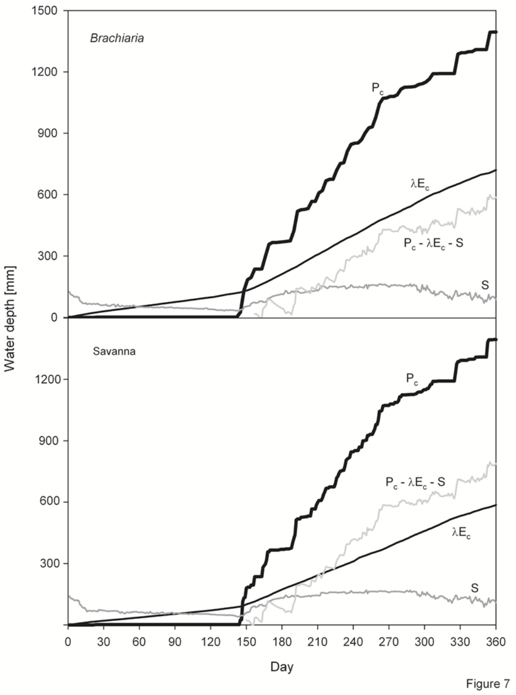

Figure 7. Trend of cumulative precipitation (Pc, thick black), cumulative evapotranspiration (Ec thin black), water storage in the first 0.5 m (S, dark grey) and balance of the previous terms (Pc – λEc – S, light grey) in a *Brachiaria* field (A) and a herbaceous savanna (B) of the Orinoco lowlands.

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