

Seasonal changes in photosynthesis and water-use efficiency of savanna species and eucalypts in Venezuela

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ABSTRACT: Eucalypt plantations in Venezuela occupy 14% of land covered by savannas. Since water use by plantations in the savannas of Mapire (Venezuelan Llanos) was apparently similar to or lower than in the natural vegetation, evaluating how carbon fixation by plantations compares to the natural vegetation could help to elucidate whether plantations have higher water-use efficiency (WUE) than the savanna. We aimed to determine, using measurements of leaf gas exchange, the seasonal changes in photosynthetic rate (P_N) and WUE of a seasonally dry savanna in Mapire, composed mainly of the grass *Trachypogon vestitus* and the tree *Curatella americana*, and trees of *Eucalyptus urophylla* growing in an experimental plantation. Daily integrated WUE (WUE_{int}) was highest in *C. americana* and similar between *T. vestitus* and *E. urophylla* during both seasons. The Gross carbon fixation (GCF) at the leaf level in *T. vestitus* was similar to *C. americana* and lower than *E. urophylla* during the dry season, whereas during the rainy season it was nearly as high as in *E. urophylla* and both higher than *C. americana*. Gross carbon fixation (GCF) in *T. vestitus* was higher than in *C. americana*, but lower than in *E. urophylla* during the dry season, while it was much higher than the other two species during the rainy season. The contribution to savanna GCF of *C. americana* was small and constant throughout the seasons. The GCF in eucalypts was 15% higher than in the savanna during the dry season, but 45% lower during the rainy season, GCF averaging 85% of that in the savanna. Since water use by plantations is lower than in the savanna, they have a large potential for C sequestration without significantly altering ground water availability.

KEYWORDS: dry season, gross primary production, rainy season.

INTRODUCTION

In Venezuela, 30,000 km² of land is covered by savannas, of which 410,000 ha have been planted with several species and hybrids of *Eucalyptus*, indicating an important change in land use that needs to be evaluated. Near the town of Mapire, Estado Anzoátegui, *Eucalyptus urophylla* has been planted at a density of 1,111 trees ha⁻¹ (González et al. 2005) for lumber and pulp production.

Eucalypt plantations in Mapire are surrounded by natural savannas composed mainly by *Trachypogon vestitus* (C₄ grass) and *Curatella americana* (C₃ evergreen tree), which are the most important grass and arboreal components of the ecosystem

(Dezzeo et al. 2008). Given the extent of these savannas and the importance for the ecosystem of photosynthetic performance of its constituents, determining the seasonal changes in photosynthetic rate (P_N) and water-use efficiency (WUE) could provide a basis for larger-scale studies. Afforestation, the planting of forest species not previously present in the ecosystem, may be an alternative for C sequestration, but its impact on the natural vegetation needs to be assessed.

A few reports on leaf gas exchange have been published for *T. vestitus* and *C. americana* in Venezuelan savannas, e.g. those by Goldstein et al. (1989), Medina and Francisco (1994) and Baruch and Bilbao (1999), whereas for *E. urophylla* in

Venezuela we are aware of only one (Herrera et al. 2012). Water vapour fluxes were measured by the eddy covariance technique in a savanna dominated by *T. vestitus* with scant tree cover in Estado Monagas, Venezuela, but no data on CO₂ fluxes were provided (San José et al. 2008). A previous study (Herrera et al. 2012) found that soil water availability did not apparently affect transpiration in trees of *C. americana* and *E. urophylla*, whereas in tussocks of *T. vestitus* transpiration and leaf area index (LAI) were markedly increased by rains. In addition, it was found that eucalypts used as much water during the dry as the rainy season and that transpiration in the savanna (the sum of the water transpired by the savanna species) increased during the rainy season, due mainly to transpiration by *T. vestitus*, and was twice as high as in eucalypts. Results suggested that the possible threats posed by eucalypt plantations to groundwater availability were not justified.

Knowledge of the WUE of the natural vegetation and the eucalypts is an important issue when afforestation is considered. Stable carbon isotope composition ($\delta^{13}\text{C}$) is a measure of long-term integrated WUE (Farquhar et al. 1989), as it can be calculated using values of $\delta^{13}\text{C}$ and leaf-air water-vapour saturation deficit (D). In *E. urophylla* and *T. vestitus*, but not in *C. americana*, stomatal conductance (g_s) proved sensitive to D (Herrera et al. 2012), which could modify the ratio intercellular to ambient CO₂ concentration (C_i/C_a) and consequently WUE; therefore, inter-specific and seasonal differences in WUE and $\delta^{13}\text{C}$ values can be expected in the savanna, as well as the plantations. Here we examine the seasonal responses of P_N to photon flux density (PFD), C_i/C_a and g_s , and how they may affect WUE through their effects on P_N . We did daily courses of gas exchange in leaves of *T. vestitus*, *C. americana* and *E. urophylla* and determined leaf $\delta^{13}\text{C}$ during the dry and the rainy season.

Based on this, we aimed to compare the stand scale gross primary production (GPP) of the savanna with that of eucalypt trees in commercial plantations in Mapire. We hypothesized that: (1) in *T. vestitus*, GPP would increase during the rainy season due to an increase in P_N and LAI; (2) in *C. americana* and *E. urophylla*, major seasonal changes in GPP would not be found; and (3) WUE would be higher in *E. urophylla* than in the savanna species, as long as P_N was higher too, because of the sensitivity of g_s to D and the previously determined lower water use in eucalypts.

MATERIAL AND METHODS

Field site and plant material: Plantations of *E. urophylla* consist of 1,111 trees ha⁻¹ planted in 1995 with a mean diameter at breast height of 0.20 m and a mean tree height of 12 m. For safety reasons, measurements in eucalypts were not carried out in plantations; instead, five trees of *Eucalyptus urophylla* S.T.

Blake, with an average diameter of 0.35 m and a height of 15 m, experimentally planted in an area of approximately 120 m², were used for measurements; trees stood isolated at an approximate distance of 5–10 m from each other. The location was the Ricardo Alfonso Rojas Experimental and Technical School, Mapire, Estado Anzoátegui (Venezuela) at 7° 42'N, 64° 46'W. In a nearby savanna, measurements were made in tussocks of *Trachypogon vestitus* Andersson (approximately 0.5 m high) and trees of *Curatella americana* L. (mean height, 7.6 ± 0.3 m). Measurements were made from January to October 2008.

Rainfall and microclimatic variables: Rainfall data for two weather stations near the study site were obtained from the Instituto Nacional de Meteorología e Hidrología (INAMEH, Venezuela). The PFD was measured with a 190-S quantum sensor connected to a LI-185 meter (LI-COR Inc., Lincoln, NE). Measurements were made during both seasons in the open (savanna and experimental plantation) and under the shade of the plantation only during the dry season. In the experimental plantation, air temperature and relative humidity were measured using two HOBO Pro V2 loggers and data dumped with a HOBO Waterproof Shuttle (Onset Computer Corporation, Pocasset, MA). In the savanna, air temperature was measured with HOBOs or with YSI 405 thermistors connected to a telethermometer (Yellow Springs Instruments, Ohio, USA) and relative humidity with HOBOs or a hair strand hygrometer (Abbeon mod. AB167B, Santa Barbara, CA). Leaf temperature was measured with YSI 409 thermistors for the calculation of D .

Leaf gas exchange: P_N , g_s and transpiration rate (E) were measured ($n=6$) with both a CIRAS 2 IRGA connected to a PLC(B) chamber (PP Systems, Hoddesdon, UK) and an LC4 IRGA connected to a PLC(B) chamber (Analytical Development Co., Hitchin, UK). Previous measurements determined that values obtained with both systems on the same leaves at the same time were not significantly different (Herrera et al. 2012). The CO₂ concentration was 380±20 μmol mol⁻¹. Measurements were made under full sun exposure on youngest, fully expanded, sun leaves. Light curves were constructed with the values of P_N and PFD measured with the IRGAs during the daily courses of leaf gas exchange. Since values of P_N per species on a single-leaf area basis presented here are possibly the highest because leaves were measured under full sun exposure at any time of the day, we corrected P_N for LAI and leaf angle. We used as PFD incident on leaves (PFD_{leaf}) values calculated for every hour of the day corrected for leaf angle relative to the horizontal plane (approximately -50°, 30° and 10° for *T. vestitus*, *C. americana* and *E. urophylla*, respectively) and LAI ($\text{PFD}_{\text{leaf}} = \text{PFD} \cdot e^{-\text{LAI}}$), according to the Beer-Lambert law (Jones 1983). With these values of PFD_{leaf} we then calculated P_N

from the light curves. Instantaneous WUE (IWUE) was calculated as P_N/E and daily-integrated WUE (WUE_{int}), as the ratio of integrated daily courses of modelled P_N and measured E . The GCF was estimated using values of modelled P_N for *T. vestitus* and *E. urophylla* and measured values of P_N in *C. americana*.

Stable carbon isotopic content: The $\delta^{13}C$ was determined with a precision of 0.15‰ using a ThermoFinnigan DeltaPlusXL Isotope Ratio Mass Spectrometer (San Jose, CA) and NIST 8573 (glutamic acid, US Geological Survey 40), NIST 8574 (glutamic acid, US Geological Survey 41) and spinach leaves (Paleolab, College of Marine Science of the University of South Florida) as standards.

Leaf area index and ground cover: Leaf area index and ground cover by *T. vestitus* and *C. americana* were estimated allometrically, and LAI in plantation eucalypts measured with a LAI-2000 Plant Canopy Analyzer (LI-COR, Lincoln, NE), as detailed by Herrera et al. (2012). The allometric estimation of LAI through the product of leaf area of one branch times the number of branches in one tree using the Adelaide technique (O'Grady et al. 2000) and projecting the crown area on the floor was done during the dry season in the five trees of experimental plantation. Values of LAI and ground cover for eucalypts used in scaling-up are those estimated in the commercial plantations.

Integrated CO₂ fixation at the leaf level and gross primary production: For all three species, seasonal GCF on a leaf area basis was calculated as the mean of the integrals of the daily courses of modelled P_N in January and March (dry season) and June and October (rainy season). Since plant cover varies widely on a large scale, GCF was calculated on a one-ha basis as leaf-level GCF multiplied by ground cover, and expressed as $g\ m^{-2}\ d^{-1}$. Values shown are the mean of values during the dry and the rainy season. Savanna GCF was calculated as the sum of GCF in *T. vestitus* and *C. americana*. Annual GCF was estimated from the regression of daily GCF versus rainfall using monthly rainfall data, multiplying daily GCF by 30 days of the month and integrating the annual course of GCF.

Statistic analysis: Values other than ground cover, GCF and GCF are mean \pm SE of six replicates. No variance is shown for modelled values. Significance was assessed through one- or two-way ANOVA at $p < 0.05$ using the statistical package Statistica and Duncan's *post hoc* test.

RESULTS

The rainfall pattern in the period of study was very similar to the average of previous years, resulting in a dry season from December

to April and a rainy season from May to November, with the highest rainfall occurring in June-July (for details see Herrera et al. 2012). The mean yearly rainfall recorded for 1994–2008 in the nearby weather stations was 1,591 mm. Daily mean minimum/maximum values of RH and air temperature were 49/85% and 25.5/32.9°C in the savanna, and 57/71% and 28.5/31.7°C in the eucalypt plantation.

In plants of *T. vestitus*, maximum P_N was on average 30% lower during the dry than the rainy season; C_i/C_a was highest in March and lowest in June, and IWUE was lowest in March and highest in June (Figure 1).

In *C. americana*, there were no significant differences in maximum P_N between seasons; C_i/C_a was lower during the dry than the rainy season, and IWUE was lowest in October (Figure 2).

Maximum P_N in plants of *E. urophylla* increased 30% during the rainy relative to the dry season, while C_i/C_a was lower during the dry than the rainy season, and IWUE during the rainy season had values similar to those in January and higher than in March (Figure 3). The daily courses of P_N in eucalypts during June and October were not completed because of rains; we assumed that the actual daily courses were similar because there were no significant differences in P_N between 11:00 am and 01:00 pm.

The P_N decreased with C_i/C_a in *T. vestitus*, whereas in the other two species no relationship was found; P_N increased linearly with g_s in *T. vestitus*, showed no change in *C. americana* and increased asymptotically in *E. urophylla* (Figure 4).

Daily PFD was 20% lower during the rainy than the dry season due to cloudiness, and shaded leaves of eucalypts received roughly 5% of incident PFD during the hours of the day with high irradiance (Figure 5). Measurements made during the dry season at the same time of the day in sun-exposed and shaded leaves of eucalypts revealed that P_N in shade leaves was at the most 16% that of sun leaves.

The P_N in both *T. vestitus* and *E. urophylla* increased markedly with PFD during the rainy relative to the dry season, more so in the latter species, whereas in *C. americana* P_N at any PFD was similar between seasons (Figure 6). Apparent quantum yield of CO₂ fixation was on average 0.017, 0.027 and 0.031 for *T. vestitus*, *E. urophylla* and *C. americana*, respectively. The E varied little with PFD; the regressions $E = 1.2911 + 0.0011 \times PFD$ ($r^2 = 0.28$) for *T. vestitus*, $E = 1.978 + 0.0005 \times PFD$ ($r^2 = 0.24$) for *C. americana* and $E = 1.668 + 0.0007 \times PFD$ ($r^2 = 0.15$) for *E. urophylla*.

Modelled values of P_N during the daily courses were on average 36% (*T. vestitus*) and 43% (*E. urophylla*) lower than measured values, no differences being found in *C. americana*.

Green leaf area per tussock of *T. vestitus* increased significantly with rains; consequently, LAI on a stand scale varied from 2.68 (January) to 1.62 (March), 5.08 (June) to 4.77 (October). The canopy remained apparently unchanged in trees of *E. urophylla* and *C. americana* throughout the period of study.

Measured LAI was 2.77 ± 0.38 in the commercial plantations of *E. urophylla*; LAI determined allometrically in the experimental plantation was 2.71 ± 0.17 . The LAI in *C. americana* was 1.14 ± 0.15 . Savanna live plant cover was estimated to vary in *T. vestitus* from 26,048 (January) to 15,754 (March), 49,316 (June) to 46,313 (October) m^2 leaf ha^{-1} , and remained apparently unchanged in *C. americana* at 5,862 m^2 leaf ha^{-1} .

Seasonal changes in $\delta^{13}\text{C}$, WUE_{int} , PN and GCF are shown in Figure 7. Leaf $\delta^{13}\text{C}$ remained constant throughout the

season in all three species, with values in *T. vestitus* being much higher than in the other two species.

At the leaf level, GCF in *T. vestitus* was similar to *C. americana* and lower than *E. urophylla*, during the dry season, whereas it was nearly as high as in *E. urophylla* and both higher than in *C. americana* during the rainy season. The GCF in *T. vestitus* was higher than in *C. americana*, but lower than in *E. urophylla* during the dry season, while it was much higher than the other two species during the rainy season. At the ecosystem

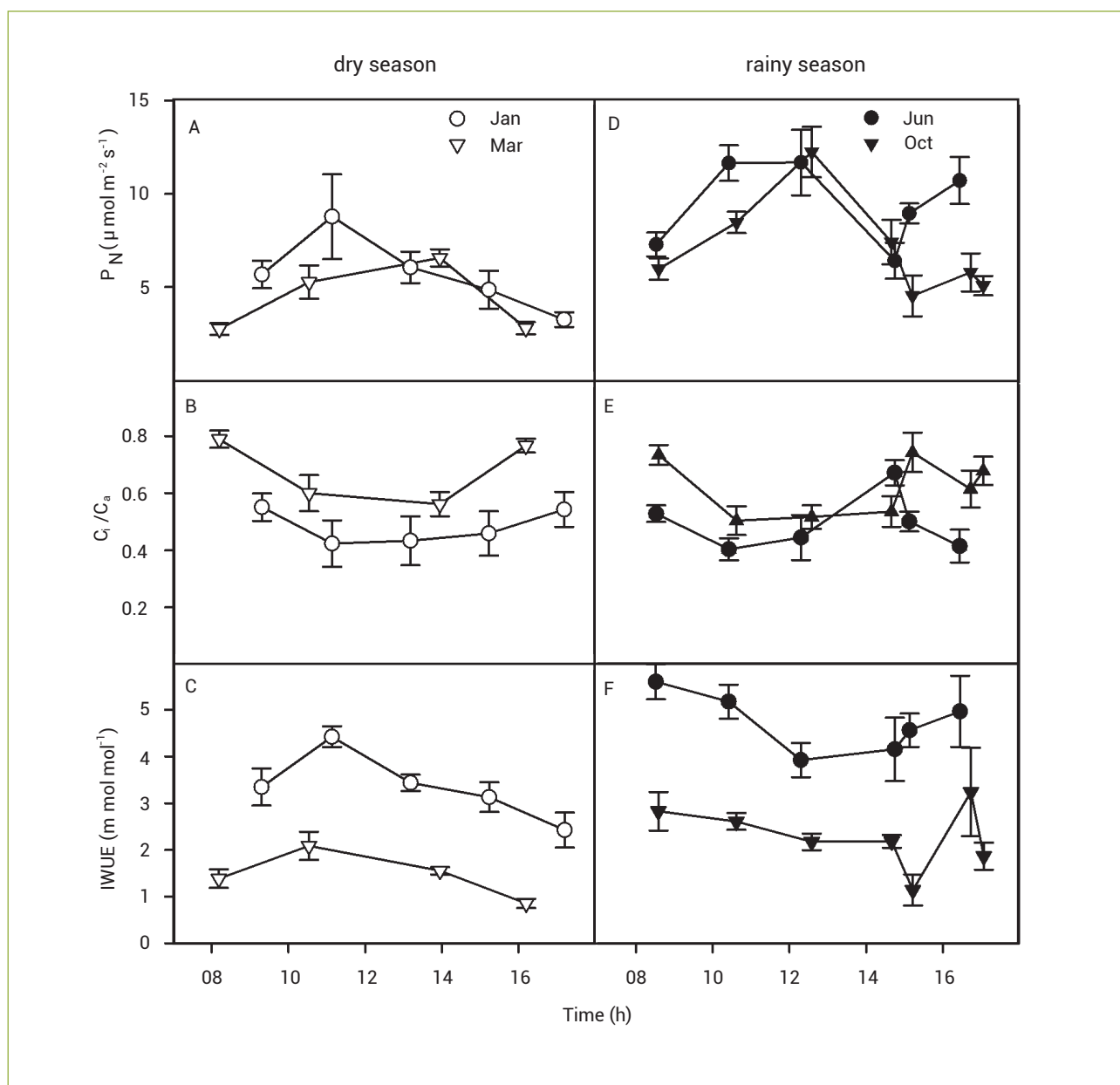


Figure 1. Seasonal changes in plants of *Trachypogon vestitus* in a daily course: (A, D) net photosynthetic rate - P_N ; (B, E) the ratio intercellular to ambient CO_2 concentration - C_i/C_a ; and (C, F) instantaneous water-use efficiency - IWUE ; Values are mean \pm SE ($n=6$). Empty symbols, dry season; filled symbols, rainy season.

level, GCF in eucalyptus was 15% higher than in the savanna during the dry season, but 45% lower during the rainy season, GCF averaging 85% of that in the savanna.

DISCUSSION

In *T. vestitus* and *E. urophylla*, but not in *C. americana*, P_N was moderately affected by drought; there were no seasonal differences in WUE_{int} within species. In what follows, we discuss responses of P_N , WUE and GCF in each species and

then proceed to compare WUE and GCF in the savanna and the plantations.

Light-saturated values of P_N in *T. vestitus* were similar during both the dry and the rainy season to values measured at $PPFD > 1,000 \mu\text{mol m}^{-2} \text{s}^{-1}$ in a Venezuelan savanna (Baruch and Bilbao, 1999).

A significant linear relation between P_N and g_s which passes through the origin in *T. vestitus* indicated co-limitation of photosynthesis by stomatal and non-stomatal factors, as

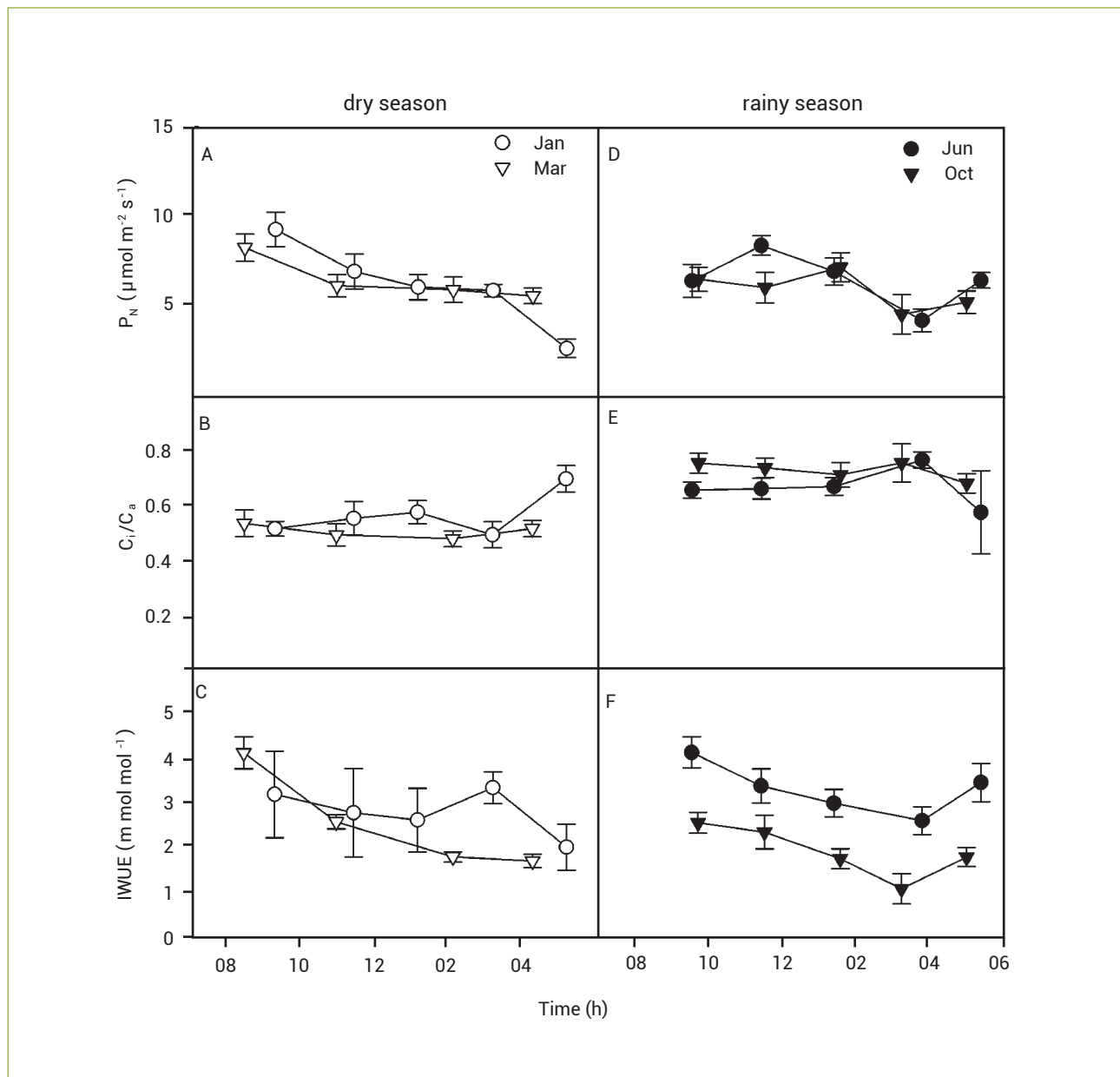


Figure 2. Seasonal changes in plants of *Trachypogon vestitus* in a daily course: (A, D) net photosynthetic rate - P_N ; (B, E) the ratio intercellular to ambient CO_2 concentration - C_i/C_a ; and (C, F) instantaneous water-use efficiency - IWUE; Values are mean \pm SE (n=6). Empty symbols, dry season; filled symbols, rainy season.

previously found in the C_4 herb *Alternanthera crucis* growing in the semi-arid regions of Venezuela (Tezara et al. 1998). This co-limitation is probably due to the compounded effects on P_N of stomatal response to D and xylem water potential, and a reduction in photosynthetic capacity with leaf age.

We compared the annual GCF of *T. vestitus* calculated from the regression of GCF versus rainfall ($7,168 \text{ g m}^{-2}$) with the green biomass of *T. vestitus* measured in a Venezuelan savanna at the end of the growing season, 261 g m^{-2} (Medina et al. 1978). Considering that the construction of 1 g leaf mass has been estimated to require

1.5 g glucose (Poorter and Grace 1997), GCF by *T. vestitus* ($1,195 \text{ g glucose m}^{-2} \text{ yr}^{-1}$) would more than satisfy the requirements to build that biomass.

Values of P_N found by us in *C. americana* are similar to those reported for other savannas in Venezuela (Medina and Francisco 1994, Goldstein et al. 1989). The P_N was apparently independent from soil water availability, as previously found in the case of g_s (Herrera et al. 2012). The independence of P_N from C_i/C_a or g_s found in *C. americana* resembles the behavior of phreatophytes growing in semi-arid environments (Tezara et al. 1998).

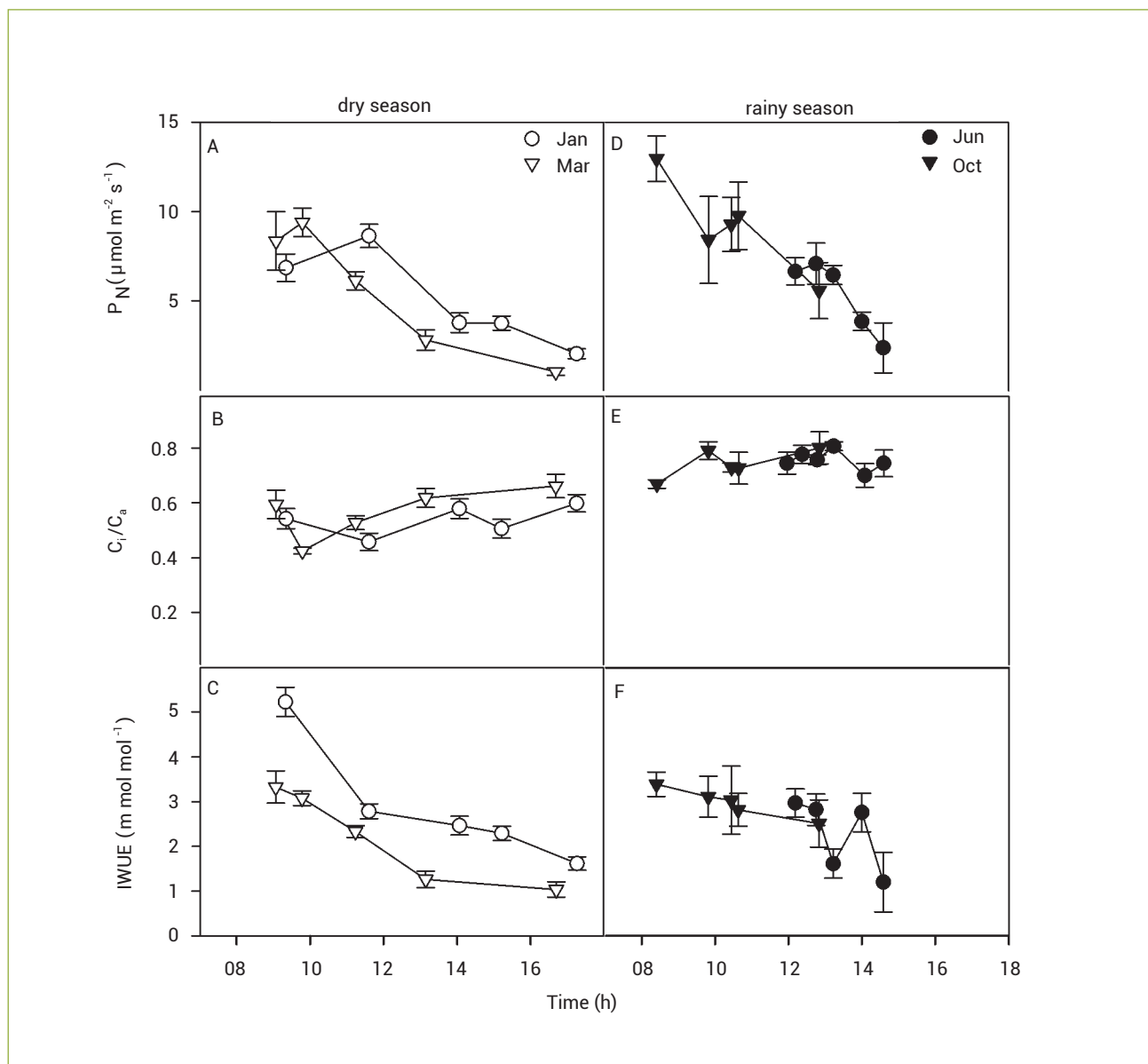


Figure 3. Figure 2. Seasonal changes in plants of *Trachypogon vestitus* in a daily course: (A, D) net photosynthetic rate - P_N ; (B, E) the ratio intercellular to ambient CO_2 concentration - C_i/C_a ; and (C, F) instantaneous water-use efficiency - IWUE. Empty symbols, dry season; filled symbols, rainy season.

Daily maximum and light-saturated P_N in *E. urophylla* were within the range for several species of *Eucalyptus*: 15.0–32.9 (mean 20.3) $\mu\text{mol m}^{-2} \text{s}^{-1}$ (Whitehead and Beadle 2004). An increase in P_N with rains may be attributed to decreased D and possibly to the occurrence of younger leaves during the rainy season. In *E. urophylla*, as opposed to *T. vestitus*, P_N was regulated mainly by g_s , rather than non-stomatal factors; the dependency of P_N with g_s in this species may be explained by the strong decrease in g_s with D previously reported in *E. urophylla* (Herrera et al. 2012) and other *Eucalyptus* species (Dye and Olbrich 1993, White et al. 2000).

Values of $\delta^{13}\text{C}$ for *E. urophylla* fall on the higher end of the range reported for 43 species of *Eucalyptus* growing along an aridity gradient (Turner et al. 2008), coinciding with a high value of the annual mean specific leaf area, $9.4 \text{ m}^2 \text{ kg}^{-1}$ (Herrera et al. 2012). Both $\delta^{13}\text{C}$ and specific leaf area values of trees of *E. urophylla* growing in the Venezuelan savanna resemble eucalypt species from more mesic sites.

Our values of GCF in eucalypts are on average half the maximum of net ecosystem exchange measured by the eddy-covariance method in a eucalypt plantation in Brazil during summer, $33 \text{ g m}^{-2} \text{ d}^{-1}$ (recalculated from Cabral et al. 2011), in

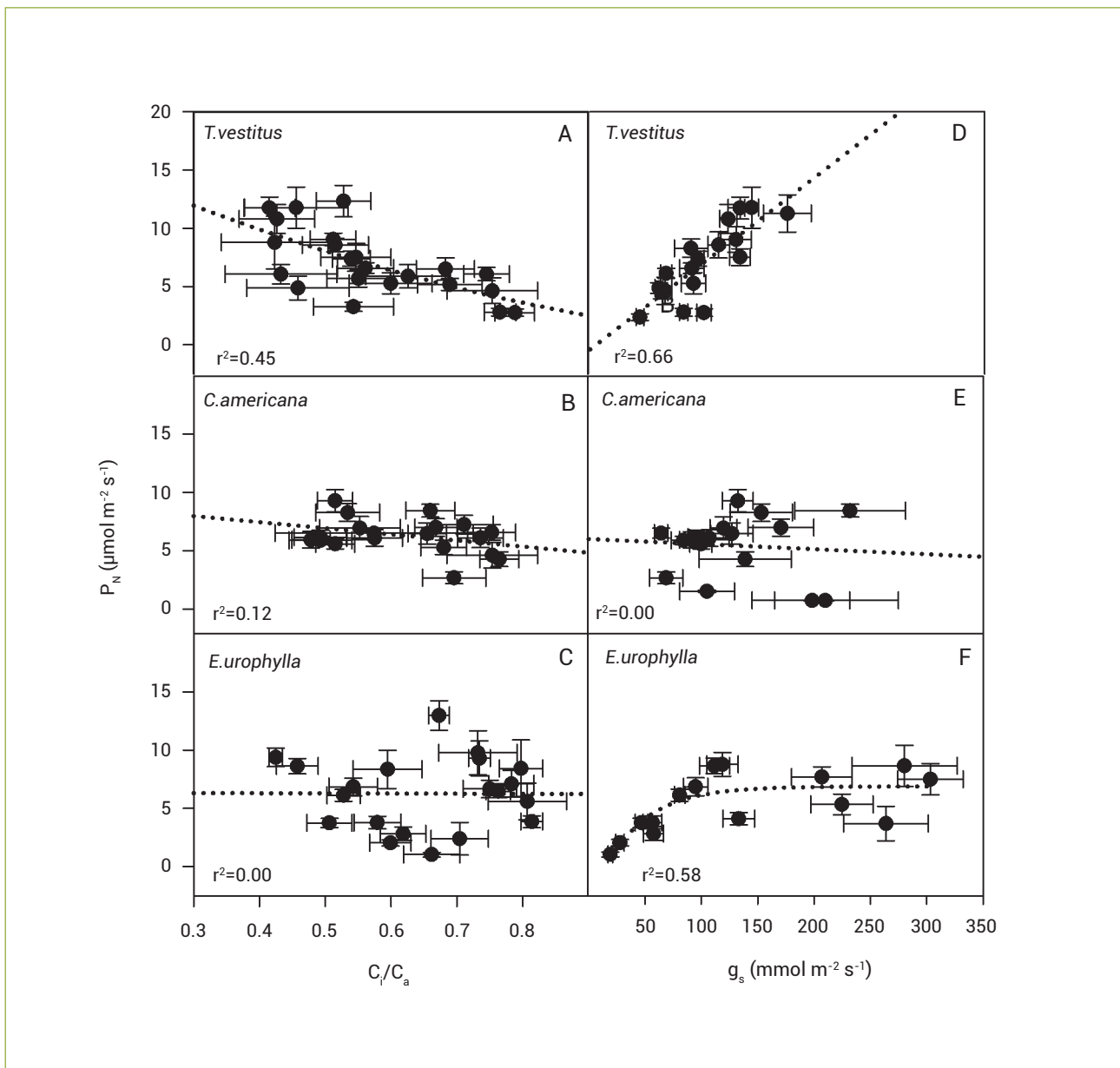


Figure 4. Change in plants of *Trachypogon vestitus*, *Curatella americana* and *Eucalyptus urophylla* of net photosynthetic rate (P_N) with the ratio intercellular to ambient CO_2 concentration (A, B, C) and stomatal conductance (D, E, F). Values are mean \pm SE (n=6).

spite of higher planting density, LAI and rainfall in our site. The differences could be due to the methods employed in each case, the eddy-covariance method giving a better integrated valued without the many assumptions of up-scaling. Besides, maximum D was 2.4 times as high in Mapire as in Brazil, which may have caused a strong stomatal closure, thus decreasing P_N .

The $\delta^{13}\text{C}$ was highest in the C_4 species *T. vestitus*, as usually is the case with plants of this CO_2 fixation pathway. In *C. americana* and *E. urophylla*, the lack of seasonal change in $\delta^{13}\text{C}$ suggests the occurrence of apparently unlimited water use during the dry season. This suggestion is supported by the absence of response of g_s to xylem water potential, as previously reported (Herrera et al. 2012). Nevertheless, the lack of difference in $\delta^{13}\text{C}$ between *C. americana* and *E. urophylla* contrasts with a higher WUE_{int} in *C. americana* than *E. urophylla* and suggests, with the lack of correspondence between $\delta^{13}\text{C}$ and WUE_{int} in *T. vestitus*, that IWUE measured during only a few days of the year is not a reliable indicator of long-term WUE. The relationship P_N versus g_s in *C. americana* and *E. urophylla* indicates that water use was not optimized, in contrast to *T. vestitus*, where co-limitation of P_N by stomatal and non-stomatal factors was evidenced by a linear regression passing through the origin (Schulze and Hall 1982).

In this study, we did a simple exercise of escalating single-leaf gas exchange measurements to the stand level, a procedure subject to uncertainties, such as actual P_N on both leaf faces, changes in incident PFD according to azimuth angle, leaf age, more frequent sampling, among others. Nevertheless, since the comparison of the savanna with eucalypts was done using

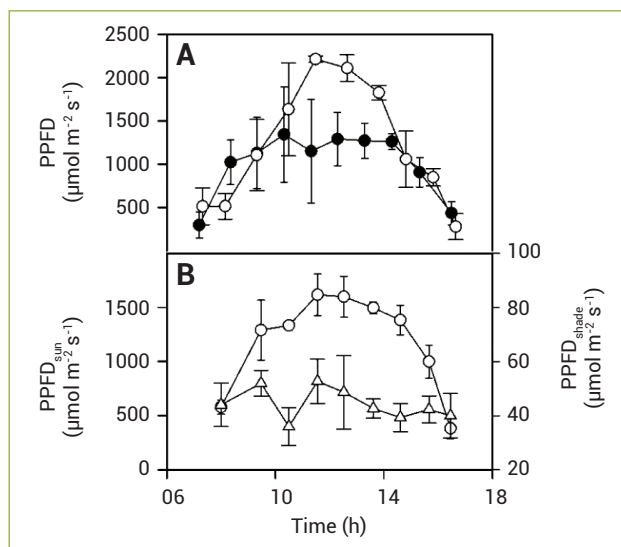


Figure 5. Daily courses of photosynthetic photon flux density incident on: (A) the savanna, and (B) sun-exposed (circles) and shaded (triangles) leaves of eucalypts. Values are mean \pm SE ($n=6$). Open symbols, dry season; closed symbols, rainy season. Note the different scale for PFD under the shade.

the same technique, our results provide a baseline for the use of more precise, global techniques, such as eddy covariance.

Values of GCF for *T. vestitus* could be underestimated, as modelled P_N values used for calculation of GCF consider only one side of the leaf. In *Styrax camporum*, a Brazilian cerrado species with both vertically and horizontally oriented leaves, the former had higher P_N than the latter (Habermann et al. 2008), and leaves where P_N was measured with a transparent assimilation chamber showed high P_N on both the adaxial and abaxial faces (Feistler and Habermann 2012). All of this suggests that the correction used by us using a vertical angle without considering light absorption by both faces throughout the day may have diminished calculated P_N .

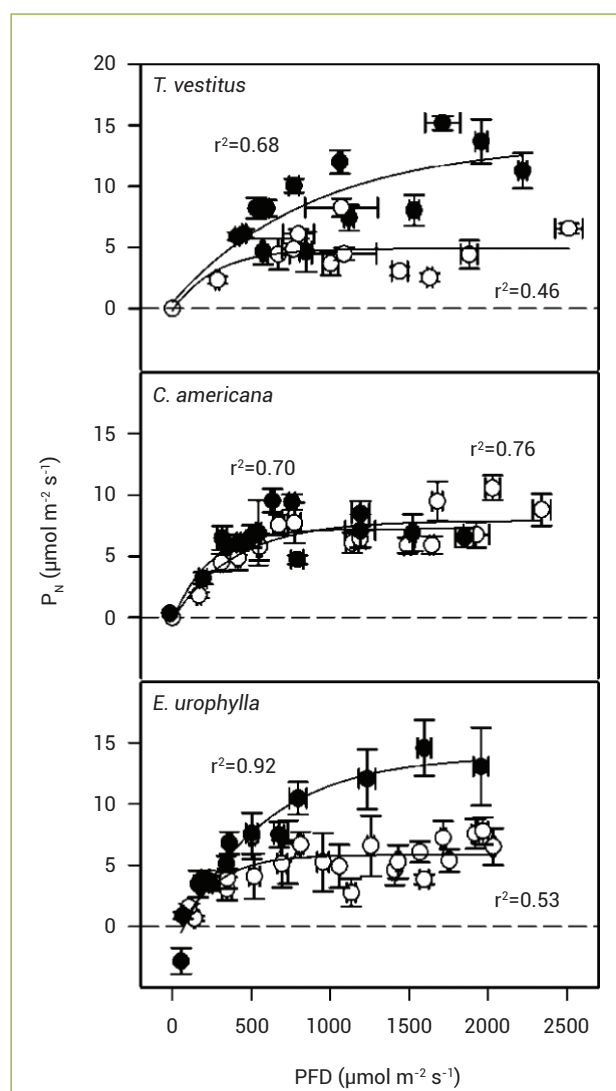


Figure 6. Seasonal changes in photosynthetic response (P_N) to photosynthetic photon flux density (PPFD) in plants of *Trachypogon vestitus*, *Curatella americana* and *Eucalyptus urophylla*. Values are mean \pm SE ($n=6$). Empty symbols, dry season; filled symbols, rainy season. The determination coefficients of the regression lines are shown ($p < 0.05$).

Standing dry biomass in *C. americana*, calculated using tree height and regressions by San José et al. (1998), was 70 Mg ha⁻¹. This figure suggests an important contribution to carbon sequestration by the savanna. A large dead biomass represented

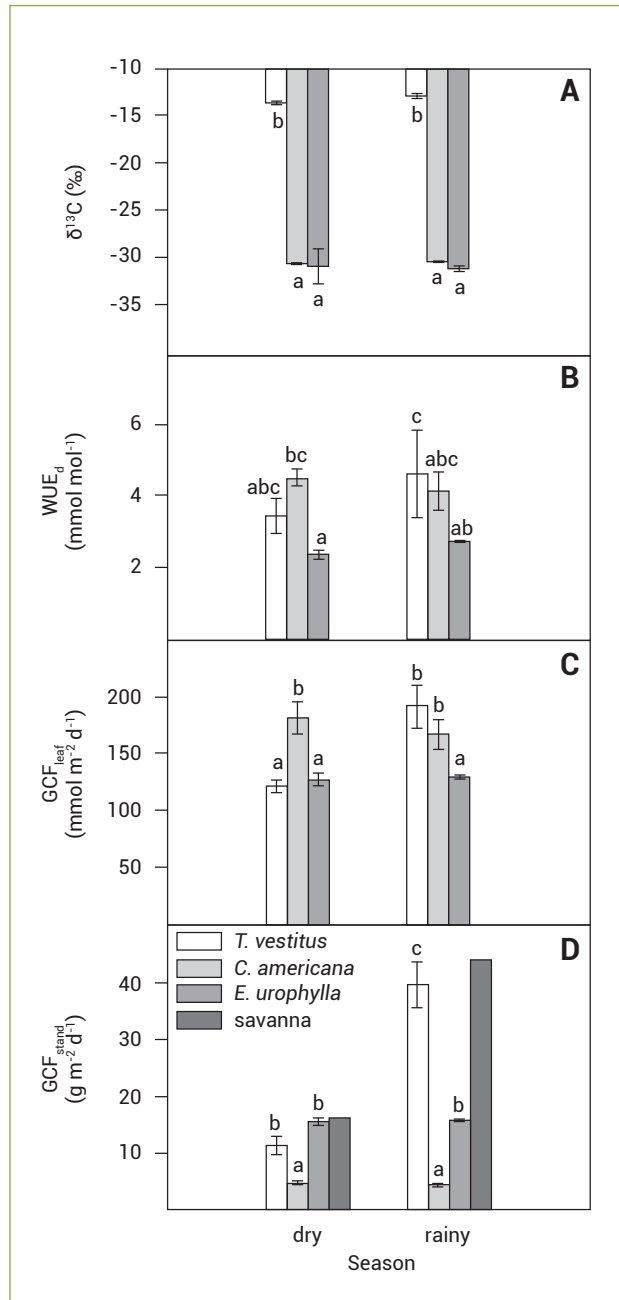


Figure 7. Seasonal changes in plants of *Trachypogon vestitus*, *Curatella americana* and *Eucalyptus urophylla* in: (A) leaf carbon isotope composition ($\delta^{13}\text{C}$); (B) instantaneous water-use efficiency integrated daily (WUE_d); (C) gross CO₂ fixation at the leaf level (GCF_{leaf}); and (D) gross CO₂ fixation (GCF_{stand}) at the ecosystem level, including the savanna. Values are mean \pm SE (n=6). Different letters indicate statistically significant differences after a two-way ANOVA (species \times season; $p < 0.05$).

by trunks of eucalypts could make a large difference in carbon sequestration with the savanna, with a smaller tree component. In a savanna in Australia, where tree density was 1,446 ha⁻¹ and mean basal area 10 m² ha⁻¹, sequestration represented 9% of total carbon stocks, of which 70% was represented by the aerial tree biomass (Cook et al. 2005). In the Mapire savanna, mean basal area comprised by *C. americana* is approximately 3 m² ha⁻¹; therefore, the sequestration potential of these trees may be even lower than in the Australian savanna. In contrast, eucalypt plantations, with basal area \sim 35 m² ha⁻¹, could make a significant contribution to sequestration.

The annual GCF in eucalypts in Mapire calculated from the regression of P_N vs rainfall was 57 Mg C ha⁻¹. Subtropical plantations of *E. urophylla* in China were shown to be large carbon sinks, with net ecosystem productivity amounting to 20 Mg C ha⁻¹ yr⁻¹ (Chen et al., 2011). If GCF in Mapire was corrected for heterotrophic respiration, net ecosystem productivity could approach the latter value. On the assumption that respiration rate during the night is similar to values of dark respiration rate from the light curves, plant CO₂ loss during the night amounts to 25 Mg C ha⁻¹ yr⁻¹, yielding a net ecosystem productivity of 32 Mg C ha⁻¹ yr⁻¹ without taking into account soil respiration. In the eastern Venezuelan savannas belonging to the same geo-morphological formation as the Mapire savannas, soil respiration rate was 7 Mg C ha⁻¹ yr⁻¹ (calculated from data of San José et al. 2003). If this value was found in the ecosystem of the present study, net ecosystem productivity in plantations would be positive and slightly higher than in China.

It has been long believed that when trees or shrubs replace pastures or grasslands, there is an automatic increase of carbon stocks. Today, it is becoming increasingly clear that this does not always happen (Albrecht and Kandji 2003). San José and Montes (2001) calculated that in the Orinoco savannas, to which our study site belongs, carbon uptake by plantations was a maximum of 4% that by tree savannas, and that carbon stock in plantations represents \sim 4% of the entire carbon stock. Carbon stocks of the savanna and the plantations should be determined before proposing that afforestation could increase carbon sequestration in a long-term compartment such as lumber for non-fuel purposes.

Savanna GCF was due mainly to *T. vestitus*, and the increase with rains in GCF due to 2.2 times higher tussock ground cover. The contribution of trees of *C. americana* was small and constant throughout the season, whereas eucalypts fixed almost as much CO₂ fixed by the savanna species. Given that they transpire less water than the savanna (Herrera et al. 2012), eucalypts could signify an important CO₂ sink that would not alter large-scale water balance. Eucalypts could be a viable option of afforestation with a view to C sequestration.

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