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Seasonal variations in leaf gas exchange of plantain cv. Hartón (Musa AAB) under different soil water conditions in a humid tropical region

R.E. Jaimez[a,*], F. Rada[b], C. García-Núñez[b], A. Azócar[b]

[a]*Instituto de Investigaciones Agropecuarias (IIAP), Facultad de Ciencias Forestales y Ambientales, Universidad de Los Andes, Apartado Postal 77 La Hechicera, Mérida 5101, Venezuela*
[b]*Instituto de Ciencias Ambientales y Ecológicas (ICAE), Facultad de Ciencias, Universidad de Los Andes, Mérida 5101, Venezuela*

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Abstract

The seasonal effect of soil water availability on leaf gas exchange of plantain plants cv. Hartón growing on two different texture soils (loamy and clayey) were evaluated. Soil water deficits corresponded to 48, 24 and 4 days without precipitation. Daily measurements of leaf gas exchange and microclimatic conditions were carried out at 2 h intervals in a humid tropical environment south of Maracaibo Lake, Venezuela. The results show that cv. Hartón is sensitive to conditions of low water deficit on loamy and to a much greater degree on clayey soils. A marked reduction in leaf conductance (g_s) was observed under severe as well as moderate deficit (below 50 mmol m^{-2} s^{-1}) on clayey soils. Under low deficit g_s increases to values between 60 and 100 mmol m^{-2} s^{-1}. The same trend was observed in plants on loamy soils but higher g_s for all conditions were obtained compared with plants on clayey soil. Stomatal closure produced a reduction of 85 and 55% of total assimilation (A_{tot}) for severe and moderate deficit in plants on clayey soils, respectively. While plants on loamy soil exhibited a 65 and 35% reduction, respectively. Water use efficiency (WUE) consistently decreased as available soil water decreased on both soil types. Independently of soil water conditions, higher WUE were always obtained for loamy soils. This suggests that cv. Hartón does not have the ability to adjust the CO_2 assimilation to transpiration ratio in order to optimize gas exchange.

* Corresponding author. Tel.: +58 274 2401587; fax: +58 274 2401575.
E-mail address: raysus@cantv.net (R.E. Jaimez).

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This evidences the importance of maintaining high conditions of available soil water in order to avoid lower assimilation rates that probably influence negatively on yield and fruit quality.

Keywords: Water deficit; Musa; Water use efficiency; Photosynthesis

1. Introduction

Soil water content is related to the variability and the quantity of precipitation of a region, frequency of watering in crops as well as to different physical properties of the soil. The capacity of the root zone to hold water and the evaporative demand of the environment are also important. The effects of soil water deficit on gas exchange of different plant species have been revised thoroughly (Hsiao, 1973; Farquhar et al., 1989). In the case of the Musaceae, the effects of water deficit have focused mainly on banana cultivars (AAA group) (Turner, 1994). Most studies have been carried out in experiments where water deficits did not exceed 2 weeks. Progressive stomatal closure has been reported when water deficit increases, giving rise to lower transpiration and CO_2 assimilation rates (Ke, 1979; Kallarackal et al., 1990; Robinson and Bower, 1988; Thomas and Turner, 1998; Turner and Thomas, 1998). Under short term soil water deficit, leaf folding increases (Turner and Lahav, 1983; Thomas and Turner, 1998), lower leaf water potentials have been reported (Hegde and Srinivas, 1989; Turner and Thomas, 1998) and in the longer term, lower leaf growth and area are obtained (Robinson and Alberts, 1986) and consequently, lower yields have been found (Robinson and Alberts, 1986; Goenaga and Irizarry, 2000).

There is very little information on the responses of cultivars with the *Musa balbisiana* (B) genome under different soil moisture and microclimatic conditions (Turner, 1995). Ekanayake et al. (1994) reported that, under field conditions, Musa with B genome have different levels of tolerance to soil water deficit. Thomas et al. (1998) have reported that an increment in the B genome confers higher resistance to drought mediated by a lower sensitivity of leaf conductance to vapor pressure difference and higher water use efficiency. Cayón et al. (1998a) under controlled laboratory conditions reported a non-significant reduction in leaf conductance and transpiration under drought conditions in plants of the cultivar Dominico–Hartón (AAB). However, assimilation rates were significantly lower in plants subjected to drought.

In Venezuela, the region south of Lake Maracaibo has the largest areas dedicated to plantain production (50,000 ha) (Cooz and Chávez, 1992). Soil and climatic characteristics of this region have allowed the successful development of this crop, but the variability and inter annual duration of dry periods on many occasions has negatively influenced production. This situation has given rise to the use of watering systems to increase yield and improve the quality of production (Nava and Villarreal, 2000). Additionally, this region is characterized by a high heterogeneity of soil types (Kijeweski et al., 1981). As a consequence, this heterogeneity introduces differences in soil water availability and in the distribution of root systems (Belalcázar et al., 1991).

In this region, there is no information on variations in gas exchange in plantain growing on different soil types and different soil moistures under field conditions. These evaluations are required to improve irrigation programs taking into account soil type and precipitation variability. Therefore, the present work evaluated leaf gas exchange in cv. Hartón plants growing on two different texture soils and under different soil water deficits set by seasonal precipitation patterns in a humid tropical environment south of Maracaibo Lake, Venezuela.

2. Materials and methods

The study site was located at Guajirita Farm, 10 km from Cuatro Esquinas, Zulia state, Venezuela (8°45′N; 71°30′W). Mean annual rainfall is 1600 mm with a bimodal regime. The wet periods are April–May and October–December (monthly rainfall above of 150 mm). Mean annual temperature is 26.8 °C with maximums between 30 and 34 °C and the minimum averages of 22–24 °C (FAV, 1984). Mean annual evaporation for the region is 1450 mm (Kijeweski et al., 1981).

Measurements were carried out on ratoon plants that had not flowered and were planted at a spacing of 3 m × 3 m (1100 plants ha^{-1}). The plants were situated in two adjacent plots with different types of inceptisols: one fluvaquentic, loamy fine, well drained and the other a fluquentic clayey fine (USDA, 1996). Plants measured in these plots were approximately 200 m apart. Characteristics of the structure and water retention capacities of these soils to −33 and −1500 kPa are given in Table 1. Plants received an annual fertilization of 80, 80 and 114 kg/ha of nitrogen, phosphorous and potassium, respectively; applied two times during the year. Black Sigatoka control was carried out with morpholine and benzimidazole in oil for both soil types.

The evaluations were carried out at three times in 2001 when different amounts of soil water were available: a severe water deficit was obtained with a period of 48 days without precipitation (2 March), a moderate deficit occurred after 24 days without precipitation (24 July) and low deficit after 4 days without precipitation (2 August). Daily precipitation and water content of three soil samples from 0 to 20 and 20 to 40 cm layers for the two soil types was determined by a gravimetric method (Gardner, 1965) throughout the measurement period (Fig. 1).

Leaf gas exchange (CO_2 assimilation (A), transpiration (E) and leaf conductance (g_s)) was measured on four plants selected randomly in each type of soil. Measurements were carried out every 2 h approximately on the central part of leaves 2–4 according to Cayón et al. (1998b) using a portable open gas exchange system (LCA-4, ADC, Hoddesdon,

Table 1
Texture, pH, water moisture percentage measured at −33 and −1500 kPa for coarse loamy and clayey soils and available soil water (ASW)

Texture type	Depth (cm)	Sand (%)	Silt (%)	Clay (%)	pH	H_2O (%)		ASW (mm)
						−33 kPa	−1500 kPa	
Coarse loamy	0–20	34	53.3	12.7	6.8	30.4	5.38	59.5
	20–40	43	50.4	6.6	6.3	28.1	2.54	56.2
Coarse clayey	0–20	13	27	60	6.3	34.0	14.3	60.0
	20–40	36	35	29	6.8	35.0	15.9	44.4

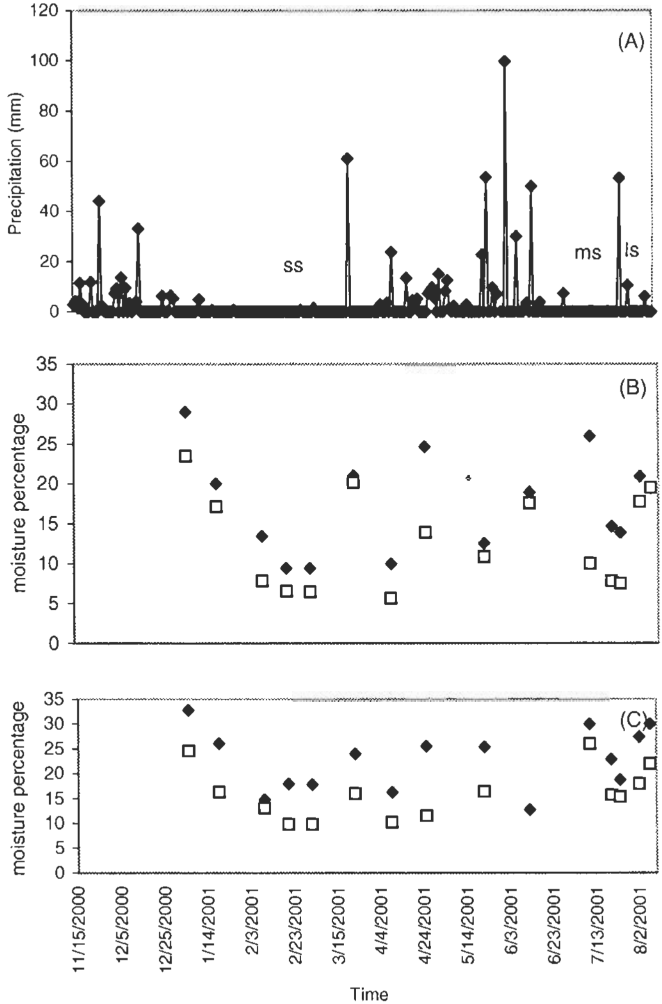

Fig. 1. Daily precipitation (A) and soil water content for loamy (B) and clayey (C) throughout the study; ss, ms and ls indicate severe, moderate and low water deficit where measurements were carried out; 0–20 cm (◆) and 20–40 cm (□) in depth.

England). Water use efficiency (WUE), defined as *A*/*E*, at the leaf level was obtained for all daily courses. Total daily transpiration (E_{tot}) and CO_2 assimilation (A_{tot}) were obtained from the integration of daily transpiration and CO_2 assimilation curves (6 h) according to Rada et al. (1996). Micrometeorological measurements were obtained simultaneously. Photon flux density (PFD) was measured with a sensor in the leaf chamber of LCA-4. Air and leaf temperatures were measured with Chromel/Alumel thermocouples (36 gauge), the latter ones attached to the lower leaf surface. Relative humidity was measured with a digital humidity meter (Extech instruments). These variables were used to determine leaf to air vapor pressure difference (VPD).

Ten plants were selected randomly at the beginning of the experiment for each of the soil types. Plantain bunches were harvested for each of these plants and weighed. These results were pooled to obtain a mean production value for each soil type.

All differences between soil types for each of the gas exchange measured variables were analyzed using Wilcoxon tests, while a *t*-test was used for fruit production differences between soil types.

3. Results

Moisture percentage was very close to that obtained at −1500 kPa for both soil textures after 48 days without precipitation, indicating low soil water availability to plants. Under moderate deficit, moisture percentage in clayey soils had hardly changed compared with severe deficit, while loamy soils showed a 33% increase in moisture percentage in the first 20 cm (Table 2). Under low deficit soil moisture percentages were well above the −1500 kPa value, with the exception of the clayey soil at 40 cm depth.

Most of the VPD values tended to be higher in plantations on clayey soil (Fig. 2). This was related to greater deficit conditions under the canopy since plants exhibited a smaller size and development, and consequently, higher leaf temperatures. A marked reduction in g_s was observed in plants under severe as well as intermediate deficit (below 50 mmol m^{-2} s^{-1}) on clayey soils; g_s of 60–100 mmol m^{-2} s^{-1} were obtained for low deficit conditions. Similarly to the results on clayey soil, g_s were higher with increasing available soil water in plants on loamy soil. For low deficit conditions values were between 280 and 350 mmol m^{-2} s^{-1}, while in conditions of moderate and severe drought these were between 250–280 and 50–250 mmol m^{-2} s^{-1}, respectively (Fig. 2). A significant decrease in g_s was displayed for most hours under all conditions of available soil water in plants on clayey soils compared to plants on loamy soil.

Lower stomatal conductance in all conditions of available soil water content strongly influenced plants of cv. Hartón growing on clayey soil giving rise to lower water losses through transpiration. E did not reach values of 1 mmol m^{-2} s^{-1} in periods of severe deficit, while in periods of moderate and low deficit they were between 1–2 and 2–3 mmol m^{-2} s^{-1}, respectively. In the case of loamy soils, E values were between 4 and 5.5 mmol m^{-2} s^{-1} (Fig. 2). Significant differences ($P \leq 0.05$) in E were found for both severe and moderate deficit when loamy and clayey soils were compared.

Lower assimilation rates were shown by plants growing on clayey soils. Under severe deficit A were always below 1 μmol m^{-2} s^{-1}. While under moderate water deficit,

Table 2
Moisture percentage at two depths for different conditions of water deficit for coarse loamy and clayey soil

Texture type	Depth (cm)	Severe deficit (3 March)	Moderate deficit (24 July)	Low deficit (2 August)
Coarse loamy	0–20	9.4 ± 1.4 (9.5)	14.0 ± 2.3 (20.5)	21.0 ± 3.7 (37.1)
	20–40	6.5 ± 2.9 (8.7)	8.5 ± 0.4 (13.1)	18.8 ± 4.9 (35.7)
Coarse clayey	0–20	17.9 ± 4.3 (11.0)	18.8 ± 4.3 (13.9)	27.5 ± 1.2(40.7)
	20–40	9.8 ± 0.4 (−14.0)	15.3 ± 4.8 (1.0)	20.0 ± 0.6 (9.6)

Values in parentheses correspond to available soil water (mm). Values are mean of three replicates ±S.E.

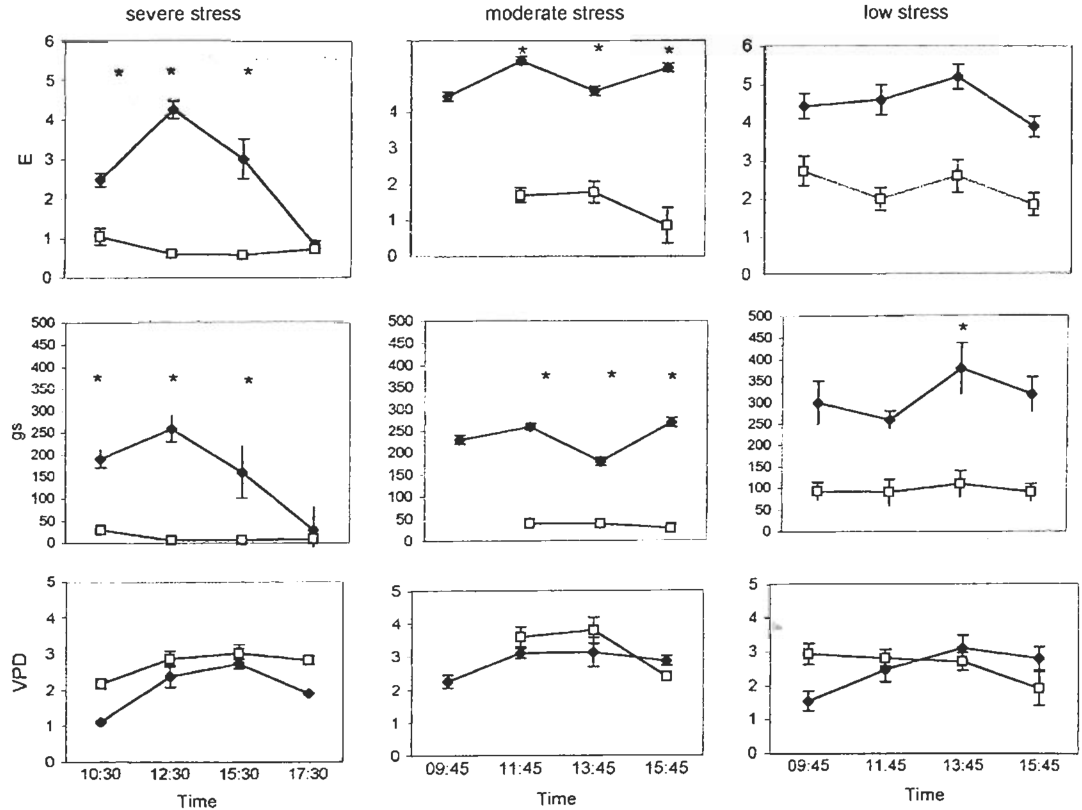

Fig. 2. Transpiration (E, mmol m^{-2} s^{-1}), leaf conductance (g_s, mmol m^{-2} s^{-1}) and VPD (kPa) for the three available water soil conditions in loamy (solid symbols) and clayey (open symbols) soils. Bars correspond to one standard error from mean. *Differences at $P < 0.05$.

maximum A values were reached in the morning (4 μmol m^{-2} s^{-1}) then declining to below 1 μmol m^{-2} s^{-1} the rest of the day. A similar pattern with higher values was obtained under low deficit, maximum A were reached in morning hours (8 μmol m^{-2} s^{-1}) decreasing along the day to values below 4 μmol m^{-2} s^{-1}. Plants on loamy soils showed lower assimilation rates under severe water deficit. In conditions of moderate and low water deficit higher assimilation rates were reached in the morning hours (14–18 μmol m^{-2} s^{-1}) and then declined to values around 6 and 12 μmol m^{-2} s^{-1}, respectively. Assimilation rates were always significantly lower ($P \leq 0.05$) for clayey compared to loamy soils in moderate and low water deficit conditions (Fig. 3). Consistently, WUE decreased as available soil water decreased on both soil types. For moderate and low water deficit conditions, higher WUE were always obtained for loamy soils. Under severe water deficit significantly lower WUE were shown by plants on clayey soil (Fig. 3).

A_{tot} was lower with increasing soil moisture deficit conditions. Higher A_{tot} was observed in plants on loamy soils for all available water soil conditions. E_{tot} showed a similar trend for clayey soil but no variations were observed between plants under moderate and low deficit in plants on loamy soils (Table 3). A close relationship between stomatal opening and assimilation rates were found when values for all deficit conditions were considered (Fig. 4).

A significant difference (30% reduction, $P < 0.05$) in fruit production was obtained when we compared the two different soil types (15.9 ± 0.8 kg per plant and 11.1 ± 0.5 kg per plant) for loamy and clayey soils, respectively.

4. Discussion

The conditions of severe and moderate water deficit influence notably stomatal response, mainly for plantain plants on clayey soils. In spite of 4 days without rain for the low deficit condition and with soils that had 80% of field capacity, plants showed low assimilation and transpiration rates. It is probable that under these soil conditions recuperation of plants can be slow due to less available water. These plants exhibited less vigor and size in relation to those on loamy soils which suggests possible root penetration problems and little exploration depths in periods of water deficit (Belalcázar et al., 1991). On the other hand, plants on loamy soil exhibited a rapid response in terms of stomatal aperture under low water deficit and after a recent moderate water deficit (20 days). Additionally, in spite of 48 days without precipitation, plants still showed a reduced leaf conductance and limited assimilation and transpiration rates. In banana, under a gradual water deficit, complete stomatal closure and negligible assimilation and transpiration rates were exhibited after 30 days without watering in greenhouse conditions (Kallarackal et al., 1990); however, a rapid recovery of transpiration and assimilation rates was observed after rewatering at 50 days.

Stomatal closure is a mechanism to avoid large losses of water by transpiration. Stomatal closure has also been reported in banana after 8 days without watering under field conditions (Thomas and Turner, 1998). Kallarackal et al. (1990) under controlled conditions of rapid water deficit also reported complete stomatal closure in banana plants after 10 days without watering. This indicates that genomic groups AAA and AAB have an

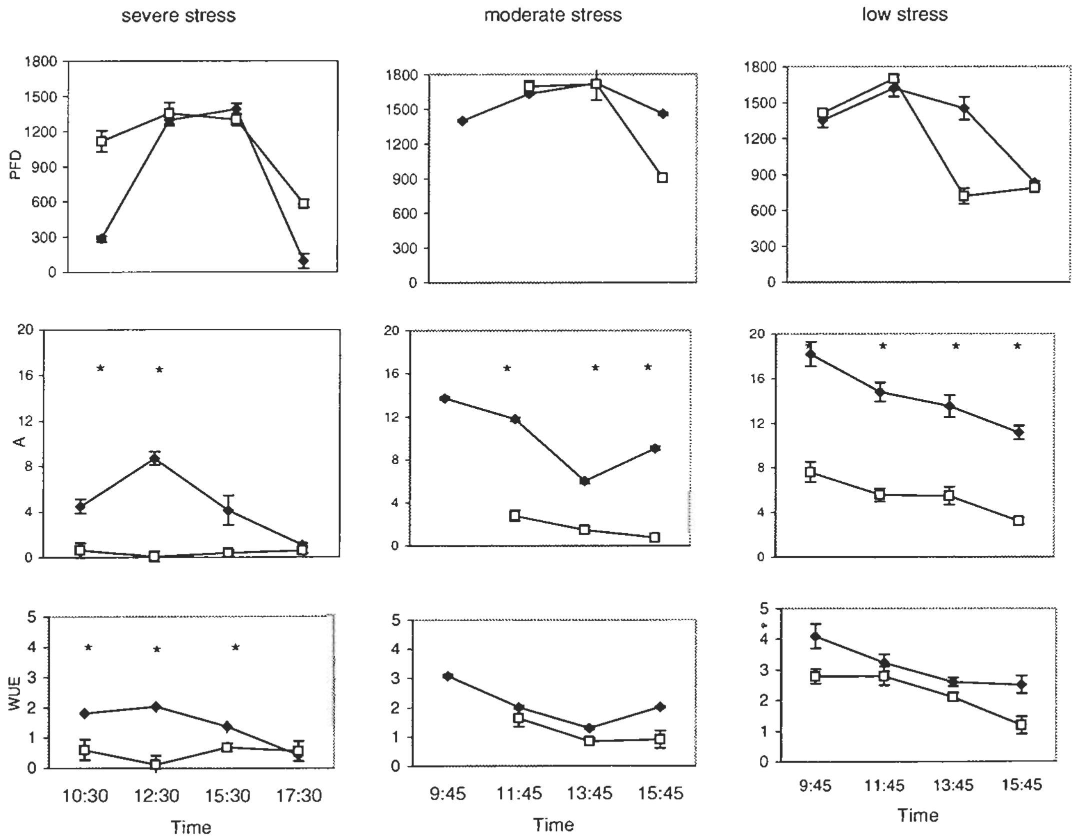

Fig. 3. PFD (μmol m^{-2} s^{-1}), CO_2 assimilation rate (A, μmol m^{-2} s^{-1}) and water use efficiency (WUE, mmol mol^{-1}) for the three available water soil conditions in loamy and clayey soils. Symbols are the same as in Fig. 2.

Table 3
Effects of soil water availability on total daily assimilation (A_{tot} mmol m^{-2} day^{-1}), transpiration (E_{tot} mol m^{-2} day^{-1}) and mean conductance (g_s mmol m^{-2} s^{-1})

Texture type	Severe deficit	Moderate deficit	Low deficit
A_{tot}			
Coarse loamy	115 ± 4	223 ± 2	345 ± 9
Coarse clayey	20 ± 6	154 ± 1.0	134 ± 0.3
E_{tot}			
Coarse loamy	53 ± 7	90 ± 11	87 ± 5
Coarse clayey	13 ± 6	28 ± 5	43 ± 6
g_s			
Coarse loamy	160 ± 40	230 ± 20	310 ± 20
Coarse clayey	10 ± 6	30 ± 7	100 ± 22

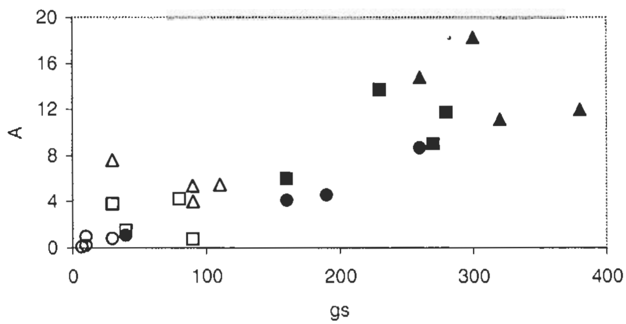

Fig. 4. Stomatal conductance-CO_2 assimilation rate relationship for low (loamy (▲) and clayey (△)) moderate (loamy (■) and clayey (□)) and severe (loamy (●) and clayey (○)) water deficit. $A = 0.041\ g_s$ $R^2 = 0.72$.

efficient mechanism to avoid excessive water deficit. This permits only small changes in water status and consequently, always maintain a high tissue water potential (Kallarackal et al., 1990). This mechanism gives the plant a quick recovery after a moderate water deficit as was shown by plants on loamy soils in our study. Thomas and Turner (1998) reported that banana plants showed higher (above 250 mmol m^{-2} s^{-1}) and rapid stomatal opening a day after watering. Little recovery presented by plants on clayey soil could, probably, be due to injury occurring at the cellular level. Inhibition in the activity of some enzymes has been described as a possible cause (Quick et al., 1989).

Reduced stomatal conductance under severe and moderate water deficit affects photosynthesis and transpiration rates. The stomatal closure produced a reduction of 65 and 35% of A_{tot} for severe and moderate deficit in plants on loamy soil, respectively, while plants on clayey soils exhibited a 85 and 55% reduction, respectively. This evidences the importance of maintaining high conditions of available soil water in order to avoid lower assimilation rates that probably influence negatively on yield and fruit quality.

The results show that cv. Hartón is sensitive to conditions of low water deficit on loamy and to a much greater degree on clayey soils. The higher assimilation rates obtained in this study (18 μmol m^{-2} s^{-1}) were similar to those reported for cv. Lady Finger (AAB)

(Thomas et al., 1998) under laboratory conditions and lower than those for cv. Dominico–Hartón (AAB) (30 μmol m^{-2} s^{-1}) under optimum water conditions in a greenhouse (Cayón et al., 1998a). These same authors find a CO_2 assimilation rate of 16 μmol m^{-2} s^{-1} in plants subjected to deficit. Cayón et al. (1991) describe maximum CO_2 assimilation rates of 14 μmol m^{-2} s^{-1} under field conditions for cv. Hartón.

Greater *E* obtained at higher VPD under low water deficit did not correspond to the *E* patterns observed under conditions of moderate to severe water deficit, this due to greater stomatal control. Similar results were reported by Thomas and Turner (1998) and Turner and Thomas (1998) in banana. These authors suggest that it may be due to a direct hydraulic feedback response on stomata, to hormonal messages or to an indirect feed-forward response becoming more prevalent under greater VPD. Similarly, low sensitivity of stomata to changes in VPD in conditions of severe deficit suggests that changes in stomatal control responds to messages from the roots (Sharp and Davies, 1989; Farquhar et al., 1989). Lower WUE obtained as available soil water decreased suggests that cv. Hartón does not have the capability to adjust this CO_2 assimilation to transpiration relationship in order to optimize gas exchange. Consequently, in the south of Maracaibo Lake region, 24 days without watering or rain will affect both CO_2 assimilation and transpiration rates of plantain plants. The effects of soil type on production were also observed in this study. Añez and Tavira (1999) and Nava and Villarreal (2000) reported similar production values (13–15 kg per plant) for cv. Hartón in studies carried out on loamy soils in nearby locations.

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