

Diurnal and seasonal patterns of leaf gas exchange in bahiagrass (*Paspalum notatum* Flüge) growing in a subtropical climate

R. V. Ribeiro*†, G. B. Lyra†, A. V. Santiago†, A. R. Pereira†, E. C. Machado* and R. F. Oliveira‡

*Centro de Pesquisa e Desenvolvimento de Ecofisiologia e Biofísica, Instituto Agronômico – IAC/Apta. C.P. 28, Campinas, SP, Brazil, †Departamento de Ciências Exatas, Escola Superior de Agricultura 'Luiz de Queiroz', Universidade de São Paulo – Esalq/USP. C.P. 09, Piracicaba, SP, Brazil, and ‡Departamento de Ciências Biológicas, Escola Superior de Agricultura 'Luiz de Queiroz', Universidade de São Paulo – Esalq/USP. C.P. 09, Piracicaba, SP, Brazil

Abstract

The objective of this study was to evaluate the seasonal and diurnal changes in leaf gas exchange in bahiagrass (*Paspalum notatum*) plants grown in an irrigated lawn. Carbon dioxide assimilation, transpiration, stomatal conductance, leaf temperature and leaf-to-air vapour pressure difference were measured during the daylight period from April 2003 to March 2004. The monitored environmental variables were photosynthetic photon flux density, air temperature, air relative humidity, photoperiod and sunshine rate. Factor and cluster analyses were used to select variables and to group months with similar physiological and meteorological characteristics, and three distinct periods were identified: (i) May to July: with low energetic availability, low leaf temperatures and low photosynthetic activity; (ii) September to January: with high energetic availability, high leaf temperatures and high photosynthetic activity; and (iii) April–March–August: a transient period with environmental and physiological characteristics showing intermediate values. The reduced plant development and growth during the winter season was in accordance to the lower photosynthetic activity recorded from June to August, this variable being a potential indicator of reduced phytomass production. The relationships between leaf gas exchange and seasonal growth are discussed.

Keywords: growth, photosynthesis, seasonality, stomatal conductance, transpiration

Introduction

Plant development is directly regulated by the surrounding environment, with the plant growth pattern being dependent on diurnal and/or seasonal dynamics in environmental conditions. In tropical and subtropical climates, where there are high solar radiation loads and high air temperatures, species develop and grow faster than in high latitude areas of temperate climate (Larcher, 1995). This can probably be explained by high resource and energy availabilities, which directly affect photosynthesis and respiration, the main processes responsible for plant growth (Parsons and Robson, 1982).

For grass species with a photosynthetic C₄ metabolism, high air temperatures, solar radiation and soil-water availability permit high photosynthetic rates and consequently increases in plant biomass. Rapid development of ground cover is a common characteristic in tropical and subtropical regions. However, grasses may experience some limitation to photosynthesis even under non-limiting air temperatures, solar radiation or soil moisture.

Under high evaporative demand, in which water loss rate to the atmosphere is higher than soil-water uptake rate, plants tend to reduce transpiration by closing stomata, a well-known mechanism for conservation of plant water status (Nobel, 1999). This stomatal response takes place even in well-watered plants, occurring more frequently in dry climates or seasons, i.e. winter in the southern hemisphere. In considering internal factors that can limit plant growth, it is important to consider the circadian rhythm (biological clock) and the role of phytochromes (Attridge, 1990). These proteins are very

Correspondence to: R. V. Ribeiro, Centro de Pesquisa e Desenvolvimento de Ecofisiologia e Biofísica, Instituto Agronômico – IAC. C.P. 28, 13001-970 Campinas, SP, Brazil.

E-mail: rafael@iac.sp.gov.br

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sensitive to light quality which changes throughout the year as well as during the day. Photoperiodic response of plant growth is assumed to occur, as observed by Sinclair *et al.* (2001, 2003) in bahiagrass and bermudagrass. In fact, longer days increase dry-matter (DM) production and leaf area in some grasses and cereals (Hay, 1990). It is also worth noting that daily changes in environmental conditions may impose some restrictions to gas exchange of grasses. Sudden changes in irradiance are expected to affect leaf gas exchange, especially in grasses that do not exhibit fully light saturation of photosynthesis (Larcher, 1995).

In the south-east region of Brazil, the summer months (December to February) are characterized by higher air temperatures and solar radiation, abundant rainfall and longer photoperiod when compared to winter months (June to August). In this region, the higher growth rate of grasses during summer is well correlated to the environmental conditions, when plants probably exhibit higher daily CO₂ assimilation, showing an increased growth rate. In contrast, reduced growth rates during winter may be a consequence of both exogenous and endogenous factors affecting plant development. Burton *et al.* (1988) reported a reduced biomass production of bermudagrass in the late summer and autumn in the northern hemisphere.

In spite of several studies on the growth of grasses as influenced by photoperiod and/or environmental conditions (Burton *et al.*, 1988; Hay, 1990; Sinclair *et al.*, 2001), there is no information about seasonal and diurnal patterns of leaf CO₂ assimilation, transpiration and stomatal conductance of bahiagrass under field conditions in a subtropical region. The understanding of these characteristics is fundamental for improving grass management programmes and for building a more complete frame of underlying processes regulating bahiagrass growth. This species is widespread in tropical and subtropical areas, attracting not only the attention of agronomists (Coelho and Pádua, 1997) but also of micrometeorologists (Menzel, 1996; Dugas *et al.*, 1997) who are concerned with ornamental aspects and micrometeorological changes respectively.

The main goal of this study was to investigate the diurnal and seasonal changes of leaf gas exchange in field-grown and irrigated bahiagrass, relating such variation to the surrounding environment, and to discuss the possible relationship between leaf gas exchange and seasonal growth.

Material and methods

Plant material

This study was conducted on a lawn of bahiagrass (*Paspalum notatum* Flügge) located at the University of

São Paulo, Piracicaba, SP, Brazil (22°42'S, 47°38'W, 546 m of altitude). According to the Köppen Classification, the experimental area shows a climate C_{wa} (subtropical humid), with rainy summers and dry winters, and monthly air temperature varying between 17.9°C (July) and 24.5°C (February). The experimental plot was maintained well irrigated and fertilized throughout the experimental period (April 2003 to March 2004).

Gas-exchange measurements and environmental data

Measurements of CO₂ and H₂O-vapour fluxes were taken in the youngest exposed and fully expanded leaves with an infrared gas analyser (LI-6400; LICOR, Lincoln, NE, USA). Carbon dioxide assimilation (A , $\mu\text{mol m}^{-2} \text{s}^{-1}$), transpiration (E , $\text{mmol m}^{-2} \text{s}^{-1}$) and stomatal conductance (g_s , $\text{mol m}^{-2} \text{s}^{-1}$) were calculated using the LI-6400 data analysis programme, which uses the general gas-exchange equation of Von Caemmerer and Farquhar (1981). For those measurements, two adjacent leaves were disposed in parallel inside the LI-6400 leaf chamber (6 cm² of sampled area) and gas exchange was measured under natural conditions, i.e. air temperature, light and humidity.

The CO₂ assimilation (A_i) and transpiration (E_i) were also integrated during the daylight period to estimate the actual water use efficiency (A_i/E_i) of bahiagrass leaves. Both integrations (A_i and E_i) were done according to the length of the measurement period, which varied throughout the experiment. Apparent daily quantum efficiency of CO₂ assimilation (ΦA_i) was calculated as $A_i/(\text{PPFD}_i \times 0.84)$, where PPFD_i (mol m^{-2}) is the daily integrated photosynthetic photon flux density and 0.84 is the fraction of light absorption adopted.

Meteorological records of air temperature (°C; mean, maximum and minimum) and relative humidity (RH, %) were obtained from an automatic weather station about 1 km from the experimental site. The sunshine ratio was determined using the solar bright time measured by a heliograph (Campbell-Stocks, Fuess, Germany). Daily changes in PPFD, leaf temperature (T_L , °C) and leaf-to-air vapour pressure difference (VPD_L , kPa) were monitored on each day of measurement (one per month) simultaneously with the leaf gas-exchange measurements made by the LI-6400. As the experimental plot was frequently irrigated, rainfall is not shown and not considered in this study.

Data analysis

Gas-exchange measurements were performed in six replications per sample time in each evaluation date.

Mean values (\pm s.d.) of evaluated parameters were plotted against environmental variables to study possible correlations. In addition, data were submitted to the ANOVA procedure and means were compared by the Tukey test ($P < 0.05$) when appropriate.

As an attempt to group months according to both physiological and environmental variables, factor analysis (FA) was used. This statistical multivariate approach has been used for evaluating variance or covariance of data series and can be applied to a set of variables to reduce its dimensionality, i.e. to replace a large set of correlated variables into a simpler system of uncorrelated variables (Johnson and Wichern, 1992).

In this study, the FA was applied to determine the environmental and physiological variables that show correlation with seasonal variation in photosynthetic activity. Those variables were the maximum CO₂ assimilation rate (A_{\max}), maximum transpiration rate (E_{\max}), maximum stomatal conductance ($g_{s-\max}$), maximum photosynthetic photon flux density (PPFD_{max}), maximum and minimum leaf temperature ($T_{L-\max}$ and $T_{L-\min}$ respectively), maximum and minimum leaf-to-air vapour pressure difference (VPD_{L-max} and VPD_{L-min} respectively) and photoperiod (N). The above variables were chosen due to their relationship with photosynthesis and respiration, the main mechanisms regulating plant growth. The data were normalized to a distribution with the mean value at zero and standard deviation of unity.

Factor rotation was applied, using the maximization criteria Varimax and maintaining the orthogonal factors, which resulted in more representative factors when considered individual sources of variation. As an eigenvalue of one represents the amount of variance explained by the original variable (Eder, 1989), only factors with an eigenvalue higher than one were selected. After selecting variables by FA, cluster analysis (CA) was used to group months with similar values of chosen variables. The agglomerative hierarchical method

of Ward (1963) was used, applying the Euclidian distance as a measure of dissimilarity. This method forms data groups by minimizing the dissimilarity or minimizing the sum of square deviation (SQD). In each procedure step, groups are formed so that the solution has the lowest SQD value within groups, considering all possible pairs of groups. In this way, groups showing lower SQD increases are gathered (Everity, 1991).

Results and discussion

Seasonal changes in environmental conditions

The lowest values of air temperature (T_{air}) were observed in May, June and July, when the PPFDi and N were also reduced (Table 1). In Piracicaba SP, Brazil, the weather is characterized by a cold and dry winter and by a hot and wet summer, when mean air temperature is higher than 22°C. The hottest season (summer) includes months from December to February, whereas the coldest one (winter) consists of June, July and August. Accordingly, the highest values of T_{air} , PPFDi and N were found in December (Table 1).

The minimum air temperature of 9.7°C was recorded in June and August (Table 1). This temperature was almost half of the minimum temperature found in summer (19.4°C in December and 18.6°C in February) and probably had some influence on the physiology of bahiagrass, which is well adapted to hot environments (Larcher, 1995). During the wet season (December and January), there is sharp drop in PPFD after midday due to cloud formation, which is commonly caused by strong convective air movements, as a result of the high surface heating.

Seasonal changes in leaf gas exchange

Diurnal changes in A were synchronized with changes in PPFD throughout the experimental period (Figures 1

Table 1 Seasonal changes in maximum ($T_{\text{air-max}}$), minimum ($T_{\text{air-min}}$) and mean (T_{air}) air temperature, mean air relative humidity (RH), daily integrated photosynthetic photon flux density (PPFDi), photoperiod (N) and sunshine ratio (n/N), in Piracicaba, SP, Brazil in 2003 and in January and March 2004.

Date	$T_{\text{air-max}}$ (°C)	$T_{\text{air-min}}$ (°C)	T_{air} (°C)	RH (%)	PPFDi* (mol m ⁻²)	N (h)	n/N
19 April	30.6	18.3	23.0	74.0	34.82	11.38	0.47
31 May	28.1	12.0	19.3	77.2	25.73	10.71	0.62
27 June	26.7	9.7	17.4	73.5	19.74	10.61	0.62
26 July	27.3	16.3	20.9	57.0	21.77	10.88	0.36
23 August	32.8	9.8	21.7	41.5	32.00	11.38	0.79
20 September	33.4	16.4	25.1	45.4	41.26	12.00	0.77
25 October	33.8	18.1	25.9	54.6	39.37	12.75	0.69
14 December	34.0	19.4	24.8	78.0	47.24	13.38	0.61
31 January	31.6	18.6	22.5	86.0	28.84	13.04	0.25
31 March	28.9	16.0	22.1	74.2	41.33	11.79	0.85

*PPFD was integrated during the measurement period in each day, varying throughout the experiment, as shown in Figures 1 and 2.

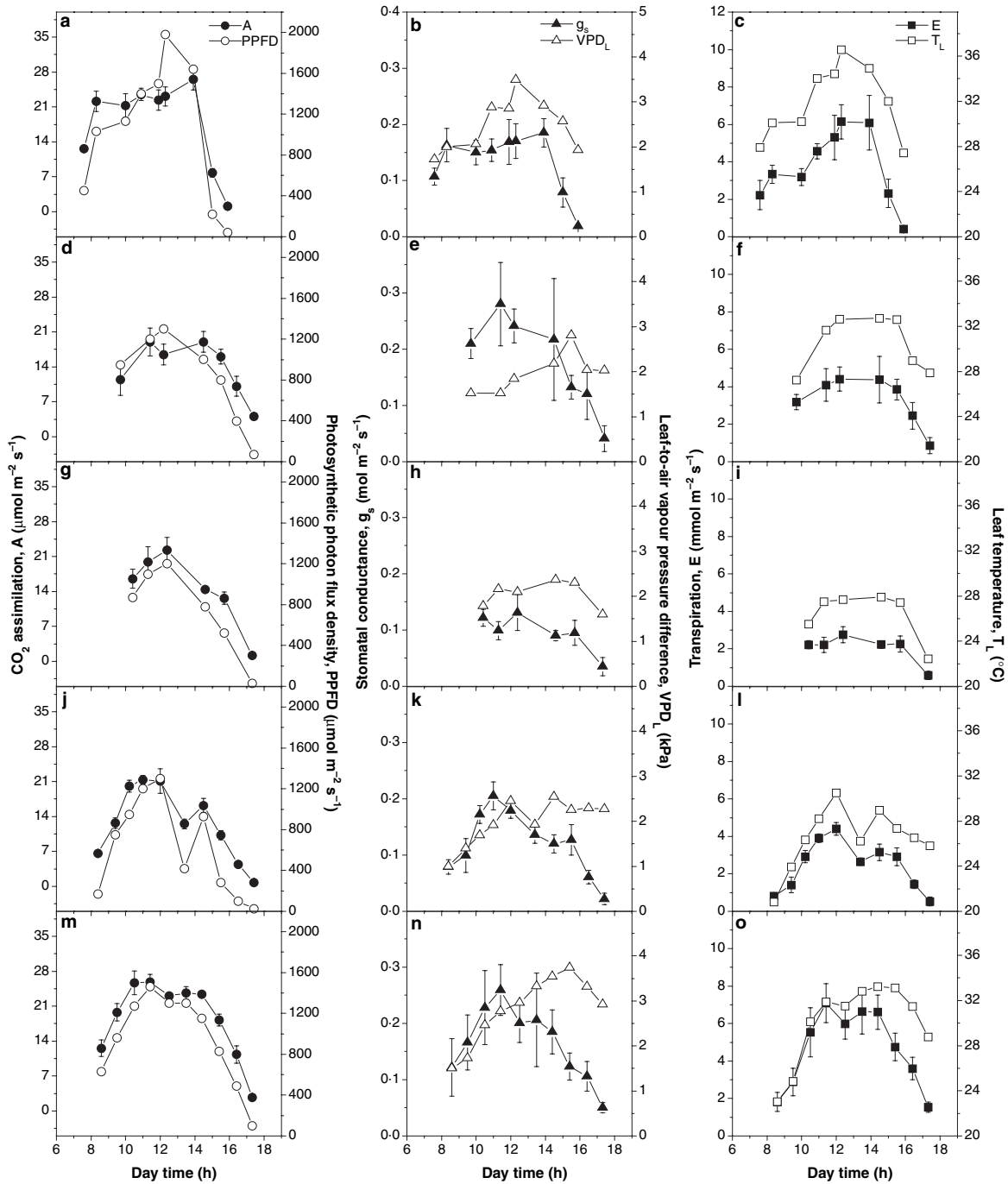


Figure 1 Diurnal changes in CO₂ assimilation (●), stomatal conductance (▲) and transpiration (■) of field-grown bahiagrass (*Paspalum notatum*) at Piracicaba, SP, Brazil. Measurements were taken in April (a–c), May (d–f), June (g–i), July (j–l) and August 2003 (m–o). Each point represents the mean value of six replicates. Standard deviations of mean are shown. Diurnal changes in photosynthetic photon flux density (○), leaf-to-air vapour pressure difference (△) and leaf temperature (□) are also shown.

and 2). Regardless of month, high *A* values were always observed around noon, when there was a high temperature and PPFD. In addition, the highest *A* values

were noticed in hot months (from September to January, Figure 2) when compared to cold ones (from May to July, Figure 1). In fact, daily mean temperatures

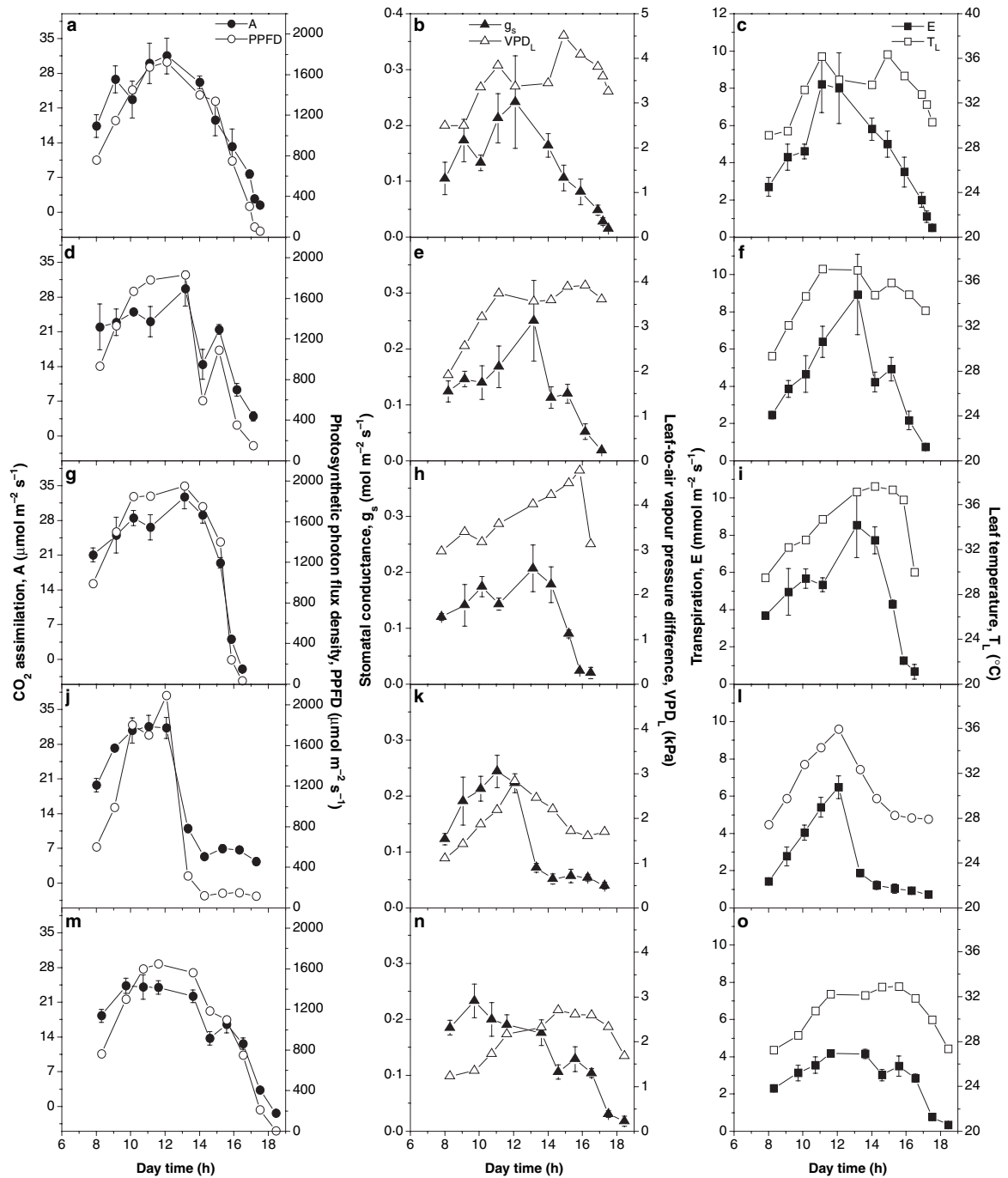


Figure 2 Diurnal changes in CO₂ assimilation (●), stomatal conductance (▲) and transpiration (■) of field-grown bahiagrass (*Paspalum notatum*) at Piracicaba, SP, Brazil. Measurements were taken in September (a–c), October (d–f), December 2003 (g–i), January (j–l) and March 2004 (m–o). Each point represents the mean value of six replicates. Standard deviations of mean are shown. Diurnal changes in photosynthetic photon flux density (○), leaf-to-air vapour pressure difference (△) and leaf temperature (□) are also shown.

varied between 22.5 and 25.9°C in hot months and between 17.4 and 20.9°C in cold ones (Table 1). Other important aspects are the minimum and maximum air temperatures reached in those months, the lowest one being registered in winter (i.e. 9.7°C in June) and the highest one in summer (i.e. 34.0°C in December).

Similar trends in g_s and A were found (Figures 1 and 2). As expected, high g_s values permit higher influx of CO₂ to carboxylation sites within the leaf and thus higher photosynthetic rates (Nobel, 1999). Curiously, those similar trends between A and g_s did not take place in June (Figure 1g and h). Even with similar diurnal environmental conditions in June and July (Figure 1g and l), the lowest g_s values were observed in June, which were different from the trend in A values when considering the measurements taken between 10:00 hours and 16:00 hours. As extremely large changes in plant canopy are necessary to modify plant photosynthesis (Sheehy *et al.*, 1977) and so its related processes, it is argued that the low g_s observed in June was induced by the environment, with the low air temperature (Table 1) during the night being a probable factor leading to reduced g_s .

Regarding temperature effects, Balasko and Smith (1971) noticed little development of switchgrass under a temperature regime of 15/10°C. From this study, Sanderson and Wolf (1995) suggested a base temperature of 10°C for growth of switchgrass (*Panicum virginatum*) under subtropical climatic conditions. As temperatures around 10°C are expected to impair plant growth, especially under subtropical conditions, the minimum air temperature of around 9.7°C in June probably caused some disturbance in the bahiagrass physiology, as noticed by reduced stomata sensitivity (Figures 1 and 2). Allen and Ort (2001) pointed out that stomatal closure following low temperatures could be a direct effect of guard cell function. In fact, 27 June 2003 had the lowest mean air temperature when compared with other dates (Table 1). The low g_s did not cause significant changes in A (Figure 1g and h) but caused a reduction in E (Figure 1i). Such an effect of low night temperature on g_s is probably dependent on diurnal temperature, as high g_s values were observed in 23 August 2003, when night temperature (before sunrise) was only 9.8°C but the mean air temperature was 21.7°C (Figure 1n and Table 1).

In spite of the decreasing g_s trend in parallel with increasing VPD_L in the afternoon, g_s values seemed to be more influenced by changing PPFD. The stomatal behaviour was very sensitive to changes in PPFD, especially during summer months when PPFD changes suddenly due to cloud formation (December and January). The highest g_s values were around 0.3 mol m⁻² s⁻¹, being recorded in May and from August to October (Figures 1 and 2).

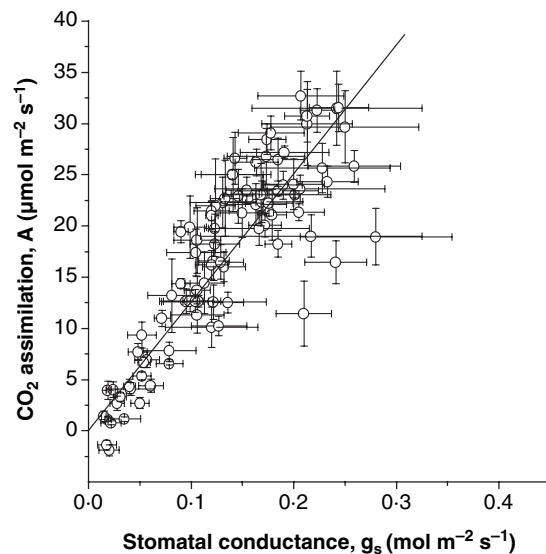


Figure 3 Leaf CO₂ assimilation as a function of stomatal conductance in field-grown bahiagrass (*Paspalum notatum*) at Piracicaba, SP, Brazil. Each point represents the mean value of six replicates from measurements taken between April 2003 and March 2004, as shown in Figures 1 and 2 (same data set). Standard deviations of mean are shown. Linear regression: $A = 125.52(g_s)$, $R^2 = 0.74$.

As transpiration (E) is directly related to g_s , these physiological variables exhibited similar diurnal changes. The highest E values were observed from September to December when the highest VPD_L values were recorded, i.e. highest evaporative demand (Figure 2). Reduced values of E in the afternoon were caused by decreased g_s , which was driven by PPFD changes (Figure 2).

A linear relationship was found between A and g_s (Figure 3), suggesting stomatal limitation of A . Such a linear relationship may also indicate that stomata are opening in response to the decreased internal CO₂ concentration caused by high photosynthetic rates (Wong *et al.*, 1979). As an attempt to verify periods of high photosynthetic activity, the maximum A values of each month were compared (Figure 4). Actually, the highest photosynthetic rates were observed from September to January, whereas the lowest ones were found in May. If stomata respond to decreased intercellular CO₂ concentration, low stomatal conductance is expected when there is low photosynthetic activity. However, the low A values did not promote reduced stomatal aperture in May (Figure 1d and e), suggesting disturbance of stomata physiology in winter.

A clear pattern among months was not found when the daily integrated CO₂ assimilation (A_i) and transpiration (E_i), actual water use efficiency (A_i/E_i) and

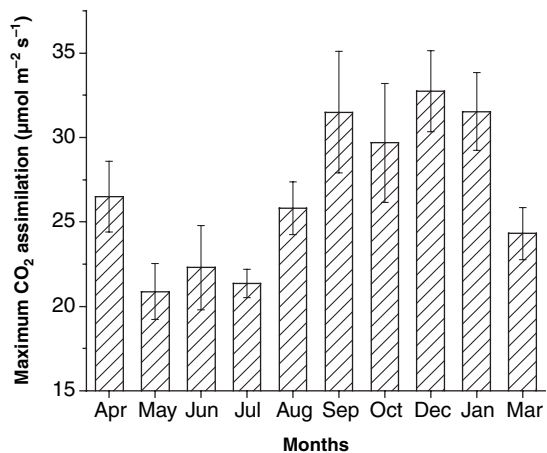


Figure 4 Maximum leaf CO₂ assimilation of field-grown bahiagrass (*Paspalum notatum*) at Piracicaba, SP, Brazil, recorded in each evaluation date from April 2003 to March 2004. Each bar represents the mean value of six replicates. Standard deviations of mean are shown.

quantum efficiency of Ai (Φ_{Ai}) were considered, as shown in Table 2. Only Ai/Ei and Φ_{Ai} can be compared throughout the experimental period due to differences in daylight period between evaluation dates (Figures 1 and 2). When Ai/Ei was considered, the months of higher efficiency were June and January, while the months with the highest Φ_{Ai} values were July and January (Table 2). The increase of Ai/Ei can be considered a common response to dry conditions of soil or atmosphere (Nobel, 1999). However, the month (considering the evaluation day) with the lowest RH (41.5%) was August (Table 1), while December exhibited the highest VPD_L values (around 4.9 kPa), as

shown in Figure 2h. The high Ai/Ei value observed in June was probably caused by the low E value in response to stomatal closure induced by low temperature (Figure 1h and Table 1). When considering Φ_{Ai} , the highest values can be obtained by an optimum balance between photosynthetic activity (Ai) and incoming PPFD (PPFDi), i.e. light-use efficiency is adjusted in relation to the available light energy to avoid over-excitation of photochemistry and consequent photoinhibition of photosynthesis (Osmond, 1994). Thus, Φ_{Ai} declined when PPFDi increased (Figure 5), revealing a regulatory mechanism for dealing with high light energy. However, it is important to differentiate photosynthetic activity and quantum efficiency, when the former is not commonly light saturated in C₄ plants and the latter is largely reduced under high light (Figure 5). Therefore, Φ_{Ai} follows the daily light energy availability regardless of seasons or months, with the exception of May (Figure 5). In this month, the environment probably induced a physiological disturbance in bahiagrass, as shown by low CO₂ assimilation, high stomatal conductance (Figure 1d and e) and low light-use efficiency (Table 2 and Figure 5).

Therefore, a simple relationship between months with similar environmental conditions and similar physiological characteristics is somewhat difficult when grasses growing under field condition in a subtropical climate were considered. Such difficulty is probably caused by the relative constancy of the evaluated physiological variables to a wide range of temperatures, a well-known characteristic of C₄ species (Ehleringer and Björkman, 1977; Larcher, 1995). As an example, switchgrass has a very broad optimum temperature range (33–41°C) for maximum CO₂ assimilation (Knapp, 1985). In addition, the influence of plant growth on photosynthesis has been reported as well as

Table 2 Seasonal changes in daily integrated CO₂ assimilation (Ai) and transpiration (Ei), actual water use efficiency (Ai/Ei) and quantum efficiency of Ai (Φ_{Ai}) of field-grown *Paspalum notatum*, in Piracicaba SP, Brazil in 2003 and in January and March 2004.

Evaluation date	Ai* (mmol m ⁻²)	Ei* (mol m ⁻²)	Ai/Ei (mmol mol ⁻¹)	Φ_{Ai}^\dagger (mmol mol ⁻¹)
19 April	589.66	121.74	4.87	20.16
31 May	422.02	101.87	4.18	19.53
27 June	381.00	53.83	7.09	22.98
26 July	441.86	86.24	5.13	24.16
23 August	625.70	157.11	4.01	23.28
20 September	755.00	174.28	4.36	21.78
25 October	626.80	159.38	3.97	18.95
14 December	754.94	169.50	4.48	19.02
31 January	609.78	93.60	6.53	25.17
31 March	637.22	111.45	5.72	18.35

Mean values are of six replicates.

*Ai and Ei were integrated during the measurement period in each day, varying throughout the experiment as shown in Figures 1 and 2.

† Φ_{Ai} is given by Ai/(PPFDi × 0.84).

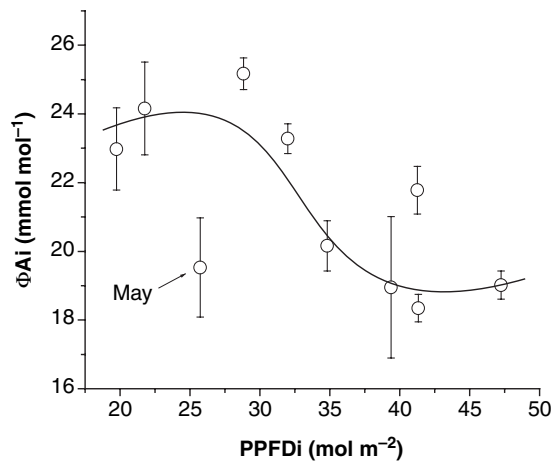


Figure 5 Quantum efficiency of daily integrated CO_2 assimilation (Φ_{Ai}) as function of daily integrated photosynthetic photon flux density (PPFDi) in field-grown bahiagrass (*Paspalum notatum*) at Piracicaba, SP, Brazil. Each point represents the mean value of six replicates from measurements taken between April 2003 and March 2004. Standard deviations of mean are shown.

the effect of photoperiod on growth and DM production (Burton *et al.*, 1988; Hay, 1990; Sinclair *et al.*, 2001, 2003). The highest A values (Figure 4), observed in months with higher photoperiod (Table 1), were probably related to the higher DM production in summer months when compared to winter months. The higher biomass production under warm conditions was verified by Balasko and Smith (1971), who observed that vigorous development of switchgrass with a day/night temperature regime of 32/26°C.

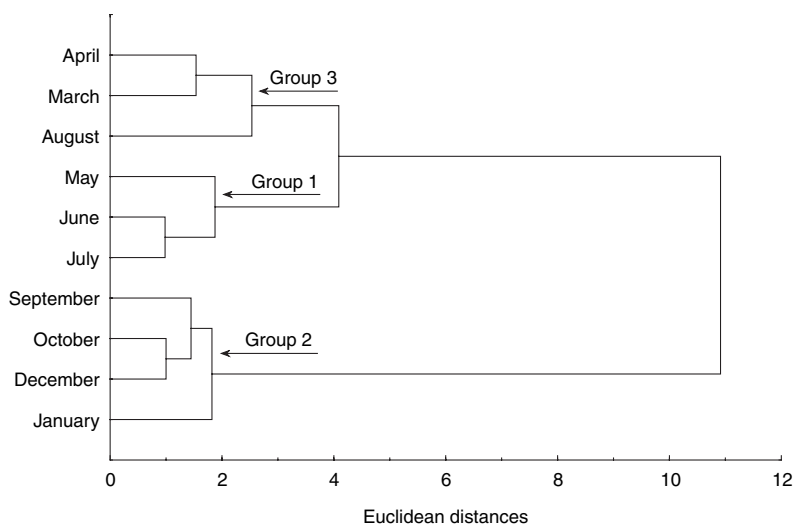


Figure 6 Dendrogram showing the month groups formed by the method of Ward (1963) based on the maximum CO_2 assimilation and maximum transpiration rates of field-grown *Paspalum notatum*, as well as maximum photosynthetic photon flux density, minimum leaf temperature and photoperiod in Piracicaba, SP, Brazil.

Grouping months with similar environmental conditions and physiological characteristics

In the FA, two factors were extracted which explained 0.799 of the total variance in the data of which factor 1 represents the major proportion of explained variance (0.527). According to the loading value (>0.86) in factor 1, the variables A_{max} , E_{max} , PPFD_{max} , $T_{\text{L-min}}$ and N were selected. Therefore, it can be argued that those variables had similar temporal variability, i.e. the seasonal variations of A_{max} and E_{max} were influenced by PPFD_{max} , $T_{\text{L-min}}$ and N .

High PPFD induces high photosynthetic activity in grasses (Morgan and Brown, 1983), causing increased biomass under high N conditions (Burton *et al.*, 1988; Hay, 1990). As daylength has a strong influence on inflorescence emergence and reproductive development (Sanderson and Wolf, 1995), it is reasonable to assume that a higher sink demand in summer due to the reproductive development could induce higher photosynthetic activity to increase carbohydrate supply. On the other hand, low diurnal $T_{\text{L-min}}$ may be a consequence of a low air temperature on the previous night in addition to the low incoming radiation during the following day, as occurred in June (Table 1). In fact, low temperatures (0–12°C) affect negatively the photosynthesis of warm-climate plants by causing impairment of carbohydrate metabolism, inhibition of ribulose-1,5-bisphosphate carboxylase (Rubisco) activity and stomatal closure (Allen and Ort, 2001). This latter response can also be involved in the reduction of diurnal transpiration, as found in June (Figure 1h and i). However, such a relationship was not found in the FA, in which the loading value for $g_{\text{s-max}}$ was less than 0.5 (data not shown). It seems that stomatal limitation

was not an important factor in determining the seasonal variation in leaf gas exchange in bahiagrass under non-limiting water supply.

The CA was carried out for grouping months with similarity between the variables extracted from factor 1. This analysis allowed the statistical identification of three groups: group 1 with low photosynthetic activity (May, June and July); group 2 with high photosynthetic activity (September, October, December and January); and group 3 with intermediate photosynthetic activity (April, August and March), as shown in Figure 6.

Group 2 was composed of months with the highest A_{\max} values ($>29.6 \mu\text{mol m}^{-2} \text{s}^{-1}$, Figure 6). The high-

est E_{\max} values were also noticed in group 2, except January which had an E_{\max} inferior to that in August (group 3). In a broad sense, high N values ($>12 \text{ h}$) were also observed in group 2 months (Table 1), as well as high diurnal $T_{L-\min}$ values ($>27.9^\circ\text{C}$) and maximum photosynthetic photon flux densities. On the other hand, the months of group 1 showed the lowest A_{\max} values ($<22.3 \mu\text{mol m}^{-2} \text{s}^{-1}$), accompanying the lowest PPFD_{\max} ($<1300 \mu\text{mol m}^{-2} \text{s}^{-1}$) and N ($<10.9 \text{ h}$) values. In group 3, the environmental and physiological variables selected had intermediate values when compared with groups 1 and 2.

When the relationship between environmental variables and leaf gas-exchange variables (A , g_s and E) was

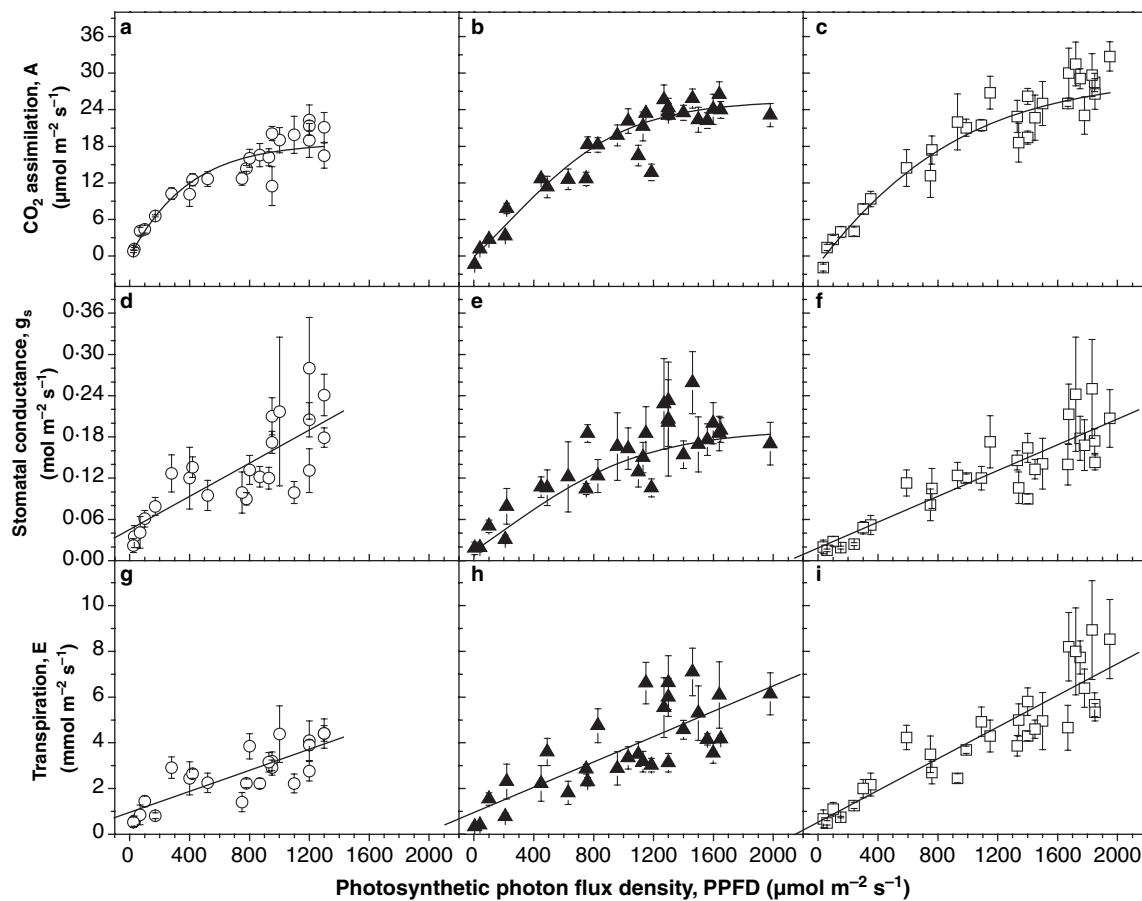


Figure 7 Leaf CO_2 assimilation (a–c), stomatal conductance (d–f) and transpiration (g–i) as functions of the incident photosynthetic photon flux density (PPFD) grouped according to the cluster analysis: low (a, d, g), intermediate (b, e, h) and high (c, f, i) photosynthetic activity. Each point represents the mean value of six replicates from measurements taken between April 2003 and March 2004, as shown in Figures 1 and 2 (same data set). Standard deviations of mean are shown. Equations of A -PPFD curves: (a) $A = 18.52 + (-198.17)/(1 + \exp(\text{PPFD} + 819.39)/361.54))$, $R^2 = 0.97$; (b) $A = 25.47 + (-39.96)/(1 + \exp(\text{PPFD} - 228.12)/395.00))$, $R^2 = 0.98$; (c) $A = 29.36 + (-116.81)/(1 + \exp(\text{PPFD} - 728.48)/708.22))$, $R^2 = 0.98$. Equations of g_s -PPFD curves: (d) $g_s = 0.0452 + 1.2077E-4(\text{PPFD})$, $R^2 = 0.62$; (e) $g_s = 0.191 + (-0.296)/(1 + \exp(\text{PPFD} - 191.58)/480.84))$, $R^2 = 0.89$; (f) $g_s = 0.0185 + 9.3803E - 5(\text{PPFD})$, $R^2 = 0.81$; Equations of E -PPFD curves: (g) $E = 0.9549 + 0.0023(\text{PPFD})$, $R^2 = 0.66$; (h) $E = 0.9476 + 0.0028(\text{PPFD})$, $R^2 = 0.63$; (i) $E = 0.5322 + 0.0035(\text{PPFD})$, $R^2 = 0.82$.

studied, it was found that only PPFD had a significant effect on those physiological variables (Figure 7). The regression coefficients were different between groups, indicating distinct responses of A , g_s and E to increase in PPFD (Figure 7).

Regarding light availability, Parsons and Robson (1982) found that the receipt of light energy was the main factor determining the pattern of CO_2 uptake. A positive relationship was observed between leaf gas-exchange variables and PPFD, with the A -PPFD curve showing less scattering of data compared to the E -PPFD and g_s -PPFD curves (Figure 7). As a typical C_4 species, bahiagrass did not exhibit light saturation of leaf gas exchange even under PPFD of $2000 \mu\text{mol m}^{-2} \text{s}^{-1}$ during summer period (Figure 7c), reaching A values around $35 \mu\text{mol m}^{-2} \text{s}^{-1}$. Morgan and Brown (1983) also found no light saturation of canopy photosynthesis in bermudagrass swards.

Curiously, the light saturation of A and g_s seems to occur in the month group with intermediate photosynthetic activity (Figure 7b, e and h). In addition, a higher data scattering of g_s was observed in the group with low photosynthetic activity (Figure 7d). With the intermediate group, the light saturation of A and g_s could be related to the phenology of bahiagrass plant, i.e. the absence of flowering and reproductive structures determining low sink demand for leaf carbohydrate and thus no stimulation of photosynthetic activity. The data scattering of g_s , found for the group with low photosynthetic activity, could be a consequence of environmental effect on stomatal physiology, i.e. low air temperature (Table 1). However, further studies should be carried out for clarifying the source-sink relationships in bahiagrass as well as the influence of specific environmental variables on bahiagrass physiology.

The quantum yield (Φ) of bahiagrass estimated from the initial (up to PPFD of $250 \mu\text{mol m}^{-2} \text{s}^{-1}$) linear region of A -PPFD curve was $0.042 (\pm 0.005 \text{ mmol CO}_2 (\mu\text{mol photon})^{-1})$. Under atmospheric O_2 concentration and air temperature of 30°C , C_4 species showed Φ values of $0.053 (\pm 0.001) \mu\text{mol CO}_2 (\mu\text{mol photon})^{-1}$ (Ehleringer and Björkman, 1977). It is important to note that such a difference is probably due to the large (diurnal) variation of environmental conditions, as data plotted in Figure 7 were recorded under different conditions, i.e. seasonal and diurnal changes of environmental variables, as shown in Figures 1 and 2.

Conclusions

When considering both physiological and meteorological variables, the results suggest three distinct periods in the year, which is in contrast to the assumption of four climatic seasons (autumn, winter, spring and summer).

In this way, we may consider three periods with the following characteristics: (i) May–June–July (group 1): a period with low energy availability, low leaf temperatures and low photosynthetic activity; (ii) September–October–December–January (group 2): a period with high energy availability, high leaf temperatures and high photosynthetic activity; and (iii) April–March–August (group 3): a transient period with environmental and physiological characteristics showing intermediate values between the first and second groups.

Considering the seasonal pattern of plant growth, bahiagrass swards have reduced plant development and growth during winter season. In fact, grass-cutting frequency is about three times higher in summer than in winter (data not shown). This is in accordance with the lower photosynthetic activity recorded from May to August, which may be a good indicator of reduced plant growth. In addition to the environmental influence, the intrinsic regulation of plant development affecting the photosynthetic activity via seasonal source-sink relationship must be considered, as suggested by the reproductive growth induced by increased daylength during the summer. For example, Woledge and Leafe (1976) found that the maximum photosynthetic rate of a ryegrass sward was higher when plants were flowering. In fact, increased leaf area and reproductive organs are also found in periods of high photosynthetic activity and energy availability.

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