

Physiological indices of seven forage species in different tropical environments

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Abstract

Forages must constantly carry out processes of adaptation to different changes in environmental factors, which leads to their physiological variables being affected. The objective was to evaluate the physiological behavior of seven tropical forage species under different environmental conditions in 2019 in Palmira, Colombia. A randomized complete block design was implemented in three localities with different altitudes, with four repetitions per species for a total of 28 experimental units per locality. An Lcpro+ portable photosynthetic measurement analyzer was used to collect data on photosynthesis rate (TA), stomatal conductance (Gs), transpiration rate (E) and Internal CO₂ (Ci). The collected data were analyzed by a comparison of means with Duncan's test ($p \leq 0.05$). The physiological indicators of the species Star, Kikuyu and the legume *Centrosema molle* in the three altitudes and the two seasons would demonstrate the mechanisms of adaptation that they develop in adverse places in which they are established.

Keywords: adaptability, altitude, forages, seasons.

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Introduction

Forages represent the main source of food for ruminants, but they are not always managed properly, due to the little knowledge available regarding the physiological behavior for their growth, as well as their nutritional composition. On the other hand, soil fertility, management and climatic conditions significantly influence grass production (Costa *et al.*, 2007). The study of the dynamics of grass ecosystems and especially their capacity to transform light energy into biomass, and of other substrates as determinants of growth has been a subject still little studied in tropical regions (Del Pozo, 2002; González, 2011).

Most of the changes that occur in the phytomass, or in the chemical constituents of the plant, over time, are limited to a growth analysis by means of empirical indices without further studying the multiple and complex functions that develop in the different morphological structures, nor in the relationships and interrelationships that are established between the production system and the environment, which are key factors for the development of management practices in forage resources (Del Pozo, 2002).

Forage production is the result of the transformation of solar energy into organic compounds through photosynthesis, where carbon from the atmosphere is combined with water and transformed into carbohydrates using solar energy (Oliveira *et al.*, 2007). Energy conversion, however, is a relatively inefficient process, as only 2 to 5% of the light energy that reaches the surface can be effectively used for canopy growth (Bernardes, 1987). Light radiation is the basic determinant of plant growth through photosynthesis and other physiological processes, such as transpiration and nutrient absorption.

The efficient use of light can be a competitive advantage for plants in the transformation of light energy into chemical energy. The intensity of light varies throughout the year, depending on the angle of radiation of the incident light (latitude) and cloudiness (Lara and Pedreira, 2011). Temperature is another important factor in photosynthesis since plants, by presenting genetic diversity and different growth and development strategies, respond better to temperature changes than to constant temperatures (Buxton and Fales, 1994). Baruch and Fisher (1991) indicate that the optimal photosynthetic activity of tropical grasses and legumes is between 35 to 39 °C and between 30 to 35 °C, respectively.

Temperatures below 0 and 20 °C would cause a low conversion of sugars in plant tissues, product of a decrease in biosynthesis processes and due to an energy deficit produced by a reduction in respiratory rate, affecting growth. Above-optimal temperatures also substantially reduce growth, due to a decrease in photosynthetic activity due to enzymatic inactivation, protein denaturation, and an increase in respiratory demand (respiration and photorespiration) (Pollock, 1990).

In addition, high temperatures increase the transpiration rate of plants and create a negative water balance that reduces cell expansion and therefore growth (Taiz and Zeiger, 2010). Due to the above, the objective of the present study was to evaluate the physiological indices of photosynthetic rate, stomatal conductance, transpiration rate and internal CO₂ in seven tropical forage species at different altitudes and seasons to identify their adaptation mechanisms.

Materials and methods

Area of study

The study was conducted in three localities in the municipality of Palmira, department of Valle del Cauca: the first in the Mario González Aranda Farm of the National University of Colombia, Palmira campus. The climate in this region is classified as tropical dry forest (Henríquez *et al.*, 2005) with average annual temperature and precipitation of 24 °C and 1 020 mm respectively and an altitude of 1 000 masl. The soil classification is Clayey (Cl) with > 19.80% sand, 0.08 of organic matter and a pH of 6.9.

The second and third localities were located in the village of La Veranera, corregimiento of Toche. The climatic classification of the area is very humid montane forest (Henríquez *et al.*, 2005) with average annual temperature and precipitation of 15 °C and 1 800 mm, respectively. The height masl varies between 1 500 and 2 000. The classification of the soil at 1 500 and 2 000 masl is Loamy (L) with >20.32% clay, organic matter 0.10 and pH 6 and in Sandy loamy (SL) with >36.32% clay, organic matter 0.26 and pH 6.1, respectively.

Experimental design, data collection and forage species

The forage species evaluated were Star (*Cynodon plectostachyus* K. Schum), Kikuyu (*Pennisetum clandestinum* Hochst. ex Chiov), Toledo (*Urochloa brizantha* Hochst. ex A. Rich. CIAT 26110), Humidicola (*Urochloa humidicola* Rendle. Schweick. CIAT 26159), Mulato II (*Urochloa hibrido*, CIAT 36087), Tanzania (*Megathyrsus max* Jacq) and *Centrosema molle* (Mart. ex Benth CIAT 15160). Twenty-eight plots of 8 m² (4*2 m) were established at 1 000, 1 500 and 2 000 masl.

Data collection was carried out by randomly selecting three healthy plants, in each of the plots of the six grasses and one legume, in the rainy and dry seasons in 2019 every 20 days between 8:00 am and 10:00 am. For each beginning of the season, a uniformity cut was made according to those suggested by Toledo and Schultze (1982). Readings of photosynthesis rate (TA) $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, stomatal conductance (G) $\text{mol m}^{-2} \text{ s}^{-1}$, transpiration rate (E) $\text{mmol m}^{-2} \text{ s}^{-1}$ and internal CO₂ (Ci) μmolmol^{-1} were made using the Lcpro+ portable photosynthetic measurement analyzer, manufactured by the company ADC Bio-Scientific in the UK.

Statistical analysis

Data collected during readings were analyzed using the general linear program (GLM) of the statistical program SAS[®] V.9.3 (SAS Institute Inc., 2011). Duncan's test ($p \leq 0.05$) was used for comparison of treatment means.

Results and discussion

Gas exchange

The statistical analysis of the data indicates that the TA by species and season presented a variation between 35.95 and 15.13 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ and 30.94 and 28.97 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ respectively (Table 1). The highest TA was observed in the species of Star, Mulato II, Toledo and Tanzania (Table 1). This is similar to those reported by Silva *et al.* (2012) in cultivars of the genus *Megathyrsus*, *Cynodon* and *Urochloa* for the same seasons in Brazil.

Table 1. Physiological indicators TA, Gs, E and Ci in forage species, altitudes, and seasons.

Species (Spe)	TA ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)	Gs ($\text{mol m}^{-2} \text{ s}^{-1}$)	E ($\text{mmol m}^{-2} \text{ s}^{-1}$)	Ci ($\mu\text{mol mol}^{-1}$)
<i>Centrosema molle</i>	15.13 a	0.99 c	7.53 cd	272.81 d
Kikuyu	28.69 b	0.82 ab	4.95 a	199.46 c
Humidicola	28.97 b	0.78 a	7.89 d	184.44 b
Tanzania	32.67 c	1 c	5.95 b	182.72 b
Toledo	3.74 d	0.95 c	6.08 b	172.11 a
Mulato II	35.12 d	0.99 c	7.02 c	172.85 a
Star	35.95 d	0.93 c	7.93 d	171.39 a
SE	2.43	0.2	0.95	14.46
Season (Se)				
Drought 1	28.97 a	0.87 a	5.49 a	201 c
Drought 2	30.46 b	0.9 a	8.36 c	183.78 a
Rain 1	30.94 b	0.95 a	5.62 a	193.6 b
Rain 2	30.35 b	0.96 a	7.6 b	193.36 b
SE	3.21	0.26	1.26	19.13
Altitude masl (Alt)				
1 000	32.75 a	1.09 a	9.06 c	209.22 c
1 500	28.12 a	0.89 b	5.95 b	192.24 b
2 000	29.67 a	0.78 c	5.3 a	179.59 a
SE	3.71	0.3	1.45	22.09
<i>p</i> -value				
Spe	< 0.0001	0.0008	< 0.0001	< 0.0001
Se	0.0042	0.2418	< 0.0001	< 0.0001
Alt	< 0.0001	< 0.0001	< 0.0001	< 0.0001
Spe * Se	< 0.0001	< 0.0001	< 0.0001	< 0.0001
Spe * Alt	< 0.0001	< 0.0001	< 0.0001	< 0.0001
Spe * Se * Alt	< 0.0001	< 0.0001	< 0.0001	< 0.0001

TA= photosynthesis rate; Gs= stomatal conductance; E= transpiration, Ci= intercellular CO₂; abcd= different literals on the same column differ significantly (Duncan ≤ 0.05).

These cultivars would have a better capacity to withstand long periods of drought and rain, in addition to being more efficient to intercept the incident energy available in these seasons by developing adaptation mechanisms by modifying the physical nature of their roots and leaves in order to regulate the entry and exit of water and CO₂ (Peters *et al.*, 2011; Silva *et al.*, 2012). The TA for Kikuyu grass was similar in the two seasons evaluated (Table 1), which would indicate its adaptability to tropical climates and its ability to photosynthesize in temperature ranges different from the one in which it is commonly found (Álvarez *et al.*, 2008).

The legume of the species *Centrosema molle* presented the lowest TA with 15.13 μmol CO₂ m⁻² s⁻¹ in both seasons. This value is above that reported by Xiong *et al.* (2017), in leguminous forages of *Trifolium repens*, where the observed value was 11.65 and 6.55 μmol CO₂ m⁻² s⁻¹ in the same seasons. The differences between these two legume species are possibly due to the environmental conditions in which they were established, allowing *Centrosema molle* to develop adaptation mechanisms conducive to the tropics.

Grasses have specific physiological and morphological characteristics that provide specific adaptation for their growth and quality. However, these undergo modifications in morphology, in yield and quality when there are changes in the climatic conditions, where temperature, solar radiation (quantity and quality), rainfall and its distribution are the components that most determine tropical conditions (Del Pozo, 2002).

The species of Star and *Centrosema molle* presented the highest and lowest TA, respectively (Table 1). This is due to the fact that Star, by having a C₄ photosynthetic pathway, presents a better adaptation to high temperatures and a low concentration of atmospheric CO₂ compared to grasses of C₃ photosynthetic pathway (Loomis and Amthor, 1999; Taylor *et al.*, 2012). The physiological explanation for this adaptation mechanism is that the C₄ photosynthetic pathway requires less Rubisco, so consequently and importantly, less foliar nitrogen (N) per leaf area unit for rapid photosynthesis.

In addition, they have a water distribution structurally different from that of C₃ plants. Allowing C₄ grasses to use water and nitrogen efficiently to achieve high growth rates, provided temperatures are adequate (Sierra, 2005; Crush and Rowarth, 2007). On the other hand, temperate grasses and tropical and temperate legumes, such as the species *Centrosema*, use the C₃ pathway to perform photosynthesis. This pathway has a highly sophisticated enzyme complex called ribulose 1,5-bisphosphate carboxylase (Rubisco), which has an affinity for oxygen (Taiz and Zeiger, 2010).

This leads to a lower rate of photosynthesis because the plant has to expend a reasonable amount of energy and nutrients to eliminate O₂. It is considered that the losses resulting from photorespiration, observed in C₃-type plants, cause a decrease between 20 and 70% of photosynthesis (Machado, 1988; Bonan, 2015).

The evaluated grasses presented different TA between them (Table 1). This is possibly due to the fact that there are structural and biochemical variations in CO₂ fixation among C₄-pathway plants (Coombes, 1988; Crush and Rowarth, 2007). Stitt *et al.* (2010) indicate that there are three types of C₄ systems, one of them is represented by plants that present Kranz-type anatomy, characterized by mesophyll parenchymal cells organized around the vascular bundle cells.

The other system is monomorphic, which occurs in a single cell and has chloroplasts with decarboxylases, as well as the enzyme Rubisco. The third C₄ system is the dimorphic system, characterized by having two types of chloroplasts, with different functionalities and biochemical processes, which allow spatial compartmentalization within a single cell (Offermann *et al.*, 2011). As for Gs and E, the highest values were observed for *Centrosema molle*, Star, Toledo, Tanzania, Mulato II and Humidicola (Table 1). Atencio *et al.* (2014) reported a higher Gs and E in *Urochloa Humidicola*, Mulato II, Toledo and Mombaza as well as a high value in the TA of these species, which presents similarity with what was reported in this work.

This would indicate that these species would have a full activity of photosynthetic processes and a better hydration condition. On the other hand, this type of results in C₄-type plants would demonstrate that an increase in atmospheric CO₂ would be beneficial to increase biomass production, as well as to reduce stomatal conductance and transpiration even when no effect on the instantaneous rate of photosynthesis is observed (Sánchez *et al.*, 2000; Pritchard and Amthor, 2005). The species *Centrosema molle*, which is a C₃-type plant, presented high values for Gs and E (Table 1).

These results can be compared with those of Guenni *et al.* (2018), which report a Gs of 0.8 mol m⁻² s⁻¹ and E of 7.2 mmol m⁻² s⁻¹ with a TA of 14.9 µmol CO₂ m⁻² s⁻¹. This may indicate that this species grew in the midst of a high concentration of atmospheric CO₂, causing an effect on the increase of the stomatal opening as an adaptation to these high levels of CO₂ (Sánchez *et al.*, 2000). The lowest values of Gs and E were observed in the species Kikuyu with 0.82 mol m⁻² s⁻¹ and 4.95 mmol m⁻² s⁻¹ respectively. According to Pereira *et al.* (2012), reduction in CO₂ assimilation rates and stomatal conductance are associated with low water potential in leaves or the reduction in water content in soil.

In addition, plants when subjected to water stress conditions reduce the efficiency of solar radiation use, which also affects photosynthesis (Taylor *et al.*, 2012; Gonçalves *et al.*, 2015). The variable C_i showed a wide variation between the species evaluated (Table 1). *Centrosema molle* and Kikuyu presented the highest value with 272.81 and 199.46 µmol mol⁻¹ respectively. This would indicate that these two forage species have a lower fixation of C_i at the time of photosynthesis due to the photorespiration process (Tolbert, 1980; Ogren, 1984), especially *Centrosema molle* which, by having a C₃ metabolism, is favored with the increase of this gas in the active site of Rubisco (Simões *et al.*, 2009).

The high C_i in Kikuyu, which has a C₄ metabolism, is possibly due to the fact that it has developed adaptation mechanisms for environments of warm climate (Taiz and Zeiger, 2010). The other species evaluated presented relatively low C_i values, confirming their condition as C₄ plants (Table 1) (Sierra, 2005; Da Matta *et al.*, 2001; Dias, 2002). Recent comparative studies of grasses have indicated that photosynthesis of C₄ species is an adaptation to low atmospheric CO₂ and open habitats, evolving at high temperatures and allowing the colonization of drier and seasonal subtropical environments with which they would have a greater efficiency in water use compared to C₃ species (Taylor *et al.*, 2012; Osborne and Freckleton, 2009).

Photosynthesis and temperature (leaf, chamber and environment) by species and altitude

Table 2 shows the general averages of TA, leaf temperature (LT), chamber temperature (CT) and air temperature for each species according to altitude.

Table 2. Average of photosynthesis rates, leaf, chamber and air temperature for each species and altitude.

Species	Altitude (m)	TA ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)	T (°C)		
			L	C	A
Star	1 000	44.5 a	45 a	39.4 a	24 a
	1 490	33.1 b	35.2 b	32.8 b	24 a
	2 000	29.4 b	29.5 c	27.2 b	22 a
Mulato II	1 000	37.1 a	39.1 a	36.6 a	24 a
	1 490	31.6 b	32.5 b	30.9 b	24 a
	2 000	36.7 a	32.1 b	29.6 b	22 a
Toledo	1 000	36.1 a	38.1 a	35.7 a	24 a
	1 490	29.4 b	31.1 b	28.8 b	24 a
	2 000	37 a	33.3 b	30.9 b	22 a
Tanzania	1 000	31.8 a	37.7 a	35.4 a	24 a
	1 490	34.2 a	33.9 b	31.9 b	24 a
	2 000	34.1 a	28.9 b	26.7 b	22 a
Humidicola	1 000	34.9 a	44.4 a	41.7 a	24 a
	1 490	26.9 b	33.1 b	30.8 b	24 a
	2 000	22.8 c	29.9 b	27.5 b	22 a
Kikuyu	1 000	27.4 b	36.9 a	34.7 a	24 a
	1 490	25.6 b	29.5 b	27.1b	24 a
	2 000	31.6 a	30.2 b	28.0b	22 a
Centrosema	1 000	14.2 a	42.3 a	39.7 a	24 a
	1 490	14.6 a	34.5 b	31.9 b	24 a
	2 000	15.6 a	31.2 b	28.9 b	22 a

TA= photosynthesis rate; T= temperature; L= leaf; C= chamber; A= environment. Different literals on the same column differ significantly (Duncan ≤ 0.05), Pr > f 0.001.

It was observed that the Star grass presented the highest TA at 1000 masl, when LT was 45 °C (Table 2). This is possibly because plants with C4 photosynthetic pathways better adapt to higher temperatures, which induce higher phosphoenolpyruvate carboxylase (PEPC) activity in this type of species (Tolbert, 1980; Ogren, 1984). Labate *et al.* (1990) indicate that photosynthetic rates in some grasses increase as temperatures increase. The cultivars Mulato II, Toledo and Humidicola obtained similar TA and temperatures, at the three altitudes.

This would indicate that they respond to an increase in temperature by increasing TA. An important aspect of temperature refers to its fluctuation, both throughout the day and throughout the year since each time it varies, the plant must adapt (Vieira and Mochel, 2010). In a study conducted by Dias (2002) in *Urochloa* sp., he observed that TA increased as temperature increased. Tanzania had a TA between 31 and 34 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ with temperatures $\geq 28^\circ\text{C}$ at the three altitudes (Table 2).

This is similar to what was reported by Mello *et al.* (2001) in the genus *Megathyrsus*, where they observed a high TA with 34.57 $\mu\text{moles CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ at an optimal temperature around 35°C . The TA of Kikuyu grass varied between 31.6 and 27.4 $\mu\text{moles CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ with temperatures between 36.9°C and 29.5°C . This coincides with what was reported by Wilen and Holt (1996) in the species *Pennisetum clandestinum*, in sub-warm environments, where the TA increased between 25°C and 40°C .

The authors indicate that this species can continue with photosynthesis at higher rates than other C4 species as temperatures decrease in autumn and winter, demonstrating its adaptability in different environments. In *Centrosema molle* no differences in TA were observed between altitudes, although temperatures were different in each (Table 2). A small reduction in TA occurred when the temperature was greater than 40°C , this could be due to the deactivation of the enzyme Rubisco that controls photosynthesis (Crafts and Salvucci, 2000). Slight decreases in TA above 35°C suggest that this species better adapts to warm climates (Baligar *et al.*, 2010).

Conclusions

The physiological indicators observed in the species Star demonstrate the adaptability of this forage at different altitudes and seasons that occur in the Colombian tropics. Kikuyu and the legume *Centrosema molle* have the ability to develop adaptive mechanisms in adverse environments in which they are commonly established.

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