Article

Physiological indices of seven forage species in different tropical environments

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Abstract

Forages must constantly carry out adaptation processes to the 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 during 2019 in Palmira, Colombia. A randomized complete block design was implemented, in three locations with different altitudes, with four repetitions per species for a total of 28 experimental units per locality. A Lcpro+ portable photosynthetic measurement analyzer was used to collect data on the photosynthesis rate, stomatal conductance, transpiration rate and internal CO_2. The data collected were analyzed using by means of a comparison of means with the Duncan test ($p \leq 0.05$). The physiological indicators of the species Estrella, Kikuyu and the legume *Centrosema molle* at the three altitudes and the two seasons would demonstrate the adaptation mechanisms that they develop in adverse places in which they settle.

Keywords: adaptability, altitude, forages, seasons.

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Introduction

Forages represent the main source of food for ruminants, but they are not always properly managed due to the little knowledge 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 pasture production (Costa *et al*., 2007). The study of the dynamics of pasture ecosystems and especially their capacity to transform light energy into biomass and of other substrates as determinants of growth has been a topic still little studied in tropical regions (González, 1993; Del Pozo, 2002).

Most of the changes that occur in the phytomass or in the chemical constituents of the plant, over time, are limited to an analysis of growth by means of empirical indices without further investigating into 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 is converted 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 in 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 transforming light energy into chemical energy. The intensity of the light varies throughout the year, depending on the radiation angle of the incident light (latitude) and the cloudiness (Lara and Pedreira, 2011). Temperature is another important factor in photosynthesis since plants, presenting genetic diversity and different growth and development strategies, respond better to changes in temperatures 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 30 to 35 °C, respectively.

Temperatures below 0 and 20 °C would cause a low conversion of sugars in plant tissues, as a result 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, with high temperatures the transpiratory rate of plants increases and a negative water balance that reduces cell expansion and therefore growth is produced (Taiz and Zeiger, 2010). Therefore, the objective of this study was to evaluate the physiological indices of photosynthetic rate, stomatal conductance, transpiration rate and internal CO_2 in seven tropical forage species at different altitudes and seasons to identify their adaptation mechanisms.

Materials and methods

Study area

The study was carried out in three localities of 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 a height above sea level of 1 000 m. The soil classification is clayey (Cl) with >19.8% of sand, 0.08 of organic matter and a pH of 6.9. The second and third localities were 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 above sea level varies between 1 500 and 2 000 m. The classification of the soil at 1 500 and 2 000 masl is loamy (L) with >20.32% of clay, organic matter 0.1 and pH 6 and in loamy-sandy (LS) with >36.32% of clay, organic matter 0.26 and pH 6.1, respectively.

Experimental design, data collection and forage species

The forage species evaluated were Estrella (*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 maximus* Jacq) and *Centrosema molle* (Mart. ex Benth CIAT 15160). Twenty-eight plots of 8 m^2 (4∗2 m) were established at 1 000, 1 500 and 2 000 masl.

The data collection was carried out by randomly selecting three healthy plants, in each of the plots of the six grasses and a legume, in the rainy and drought seasons during 2019 every 20 days between 8 am and 10 am. For each beginning of the season, a cut of uniformity was made according to that suggested by Toledo and Schultze-Kraft (1982). Readings of photosynthesis rate (PR) µmol CO_2 m^{-2} s^{-1}, stomatal conductance (G) mol m^{-2} s^{-1}, transpiration rate (E) mmol m^{-2} s^{-1} and internal CO_2 (Ci) µmolmol^{-1} were carried out by means of the Lcpro+ portable photosynthetic measurement analyzer, manufactured by the company ADC Bio-Scientific in the UK.

Statistical analysis

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

Results and discussion

Gas exchange

The statistical analysis of the data indicates that the PR by species and season had a variation between 35.95 and 15.13 µmol CO_2 m^{-2} s^{-1} and 30.94 and 28.97 µmol CO_2 m^{-2} s^{-1}, respectively, as observed in Table 1. The highest PR was observed in the species of Estrella, Mulato II, Toledo and Tanzania (Table 1). This is similar to what was reported by Silva *et al*. (2012) in the cultivars of the genus *Megathyrsus*, *Cynodon* and *Urochloa* for the same seasons in Brazil.

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

Species (Spe)	PR (µmol CO_2 m^{-2} s^{-1})	Gs (mol m^{-2} s^{-1})	E (mmol m^{-2} s^{-1})	Ci (µmol mol^{-1})
Centrosema molle	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
Estrella	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 (m)		
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
		p-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

PR= photosynthesis rate; Gs= stomatal conductance; E= transpiration; Ci= intercellular CO_2; 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 at intercepting the incident energy available during 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 CO_2 (Peters *et al*., 2011; Silva *et al*., 2012). The PR 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* had the lowest PR with 15.13 μmol CO_2 m^{-2} s^{-1} in both seasons. This value is above that reported by Xiong *et al*. (2017), in legume forages of *Trifolium repens* where the observed value was 11.65 and 6.55 μmol CO_2 m^{-2} s^{-1} at the same seasons. The differences between these two legume species are possibly due to the environmental conditions in which they settled, allowing *Centrosema molle* to develop adaptation mechanisms conducive to the tropics.

The pastures have specific physiological and morphological characteristics that provide specific adaptation for their growth and quality. However, they undergo morphological modifications, in yield and their quality when there are changes in 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 Estrella and *Centrosema molle* had the highest and lowest PR, respectively, Table1. This is because Estrella, having a C4 photosynthetic pathway, has a better adaptation to high temperatures and to a low concentration of atmospheric CO_2 compared to pastures 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 unit of leaf area for rapid photosynthesis.

In addition, they have a structurally different water distribution than C3 plants. This allows 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, as is the case of the *Centrosema* species, 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 must spend a reasonable amount of energy and nutrients to eliminate O_2. 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 grasses evaluated showed different PR between them, as perceived in Table 1. This is possibly due to the fact that, among C4-pathway plants, there are structural and biochemical variations in CO_2 fixation (Coombs, 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 have a Kranz-type anatomy, characterized by parenchymatic cells of the mesophyll organized around the cells of the vascular bundle. The other system is the monomorphic, which occur in a single cell and has chloroplasts with decarboxylases as well as the Rubisco enzyme. The third C4 system is the dimorphic system, characterized by having two types of chloroplasts, with different biochemical functionalities and processes, which allow spatial compartmentalization within a single cell (Offermann *et al*., 2011).

Regarding G_s and E, the highest values were observed for *Centrosema molle*, Estrella, Toledo, Tanzania, Mulato II and Humidicola, as analyzed in Table 1. Atencio *et al*. (2014) reported a higher G_s and E in *Urochloa* Humidicola, Mulato II, Toledo and Mombasa as well as a high value in the PR of these species, which is similar to 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 CO_2 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, had high values for G_s and E (Table 1). These results can be compared with those of Guenni *et al*. (2018), which report a G_s of 0.8 mol m^{-2} s^{-1} and E of 7.2 mmol m^{-2} s^{-1} with a PR of 14.9 µmol CO_2 m^{-2} s^{-1}. This may indicate that this species grew in the midst of a high concentration of atmospheric CO_2, causing an effect on the increase in stomatal opening as an adaptation to these high levels of CO_2 (Sánchez *et al*., 2000).

The lowest values of Gs and E were observed in the Kikuyu species 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 CO_2 assimilation rates and stomatal conductance are associated with low water potential in leaves or reduction of water content in land. In addition, plants when subjected to water stress conditions reduce the efficiency of the use of solar radiation, which also affects photosynthesis (Taylor *et al*., 2012; Gonçalves *et al*., 2015).

The Ci variable showed a wide variation between the species evaluated, as shown in Table 1. *Centrosema molle* and Kikuyu had the highest value with 272.81 and 199.46 µmol mol^{-1}, respectively. This would indicate that these two forage species have a lower Ci fixation at the time of photosynthesis due to the photorespiration process (Tolbert, 1980; Ogren, 1984), especially *Centrosema molle*, which, having a C3 metabolism, is favored with the increase of this gas in the active site of Rubisco (Simões *et al*., 2009). The high Ci in Kikuyu, which has a C4 metabolism, is possibly due to the fact that it has developed adaptation mechanisms for warm climate environments (Taiz and Zeiger, 2010).

The other species evaluated had relatively low C*i* values, which confirms their condition of C4 plants, Table 1 (Da Matta *et al*., 2001; Dias, 2002; Sierra, 2005). Recent comparative studies of grasses have indicated that the photosynthesis of C4 species is an adaptation to low atmospheric CO_2 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 the use of water compared to C3 species (Osborne and Freckleton, 2009; Taylor *et al*., 2012).

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

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

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

Species	Altitude (m)	PR (µmol CO_2 m^{-2} s^{-1})	T (ºC)		
			L	C	A
Estrella	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	34.1a	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	27.1 b	24 a
	2 000	31.6 a	30.2 b	28 b	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

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

It was observed that the Estrella grass had the highest PR at 1 000 masl, when the LT was 45 °C (Table 2). This is possibly because plants with C4 photosynthetic pathways adapt better to higher temperatures, which induce greater phosphoenolpyruvate carboxylase (PEPC) activity in these types of species (Tolbert, 1980; Ogren, 1984). Labate *et al*. (1990) indicate that photosynthetic rates in some grasses increase as temperatures rise. The cultivars Mulato II, Toledo and Humidicola obtained similar PR and temperatures, at the three altitudes.

This would indicate that they respond to an increase in temperature by increasing PR. An important aspect of temperature refers to its fluctuation, both throughout the day and throughout the year, since every time it varies, the plant must adapt, mentioned by authors such as Vieira and Mochel (2010). In a work carried out by Dias (2002) in *Urochloa sp*., it was observed that the PR increased as the temperature increased. Tanzania had a PR between 31 to 34 μmol CO_2 m^{-2} s^{-1} with temperatures ≥28 °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 PR with 34.57 μmoles CO_2 m^{-2} s^{-1} at an optimal temperature around 35 °C. The PR of Kikuyu grass varied between 31.6 and 27.4 μmoles CO_2 m^{-2} 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 PR increased between 25 °C and 40 °C.

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

Conclusions

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

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