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STOMATAL CONDUCTANCE BEHAVIOR OF TWO CUBAN TOMATO VARIETIES IN FIELD CONDITIONS AND LIMITED IRRIGATION

Comportamiento de la conductancia estomática de dos variedades de tomate cubanas en condiciones de campo y riego limitado

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ABSTRACT. It was studied the stomatal conductance (gs) behavior in tomato plants varieties INCA-17 and Amalia, cultivated in field conditions. Moisture profiles were performed at two depths 0-15 cm and 15-30 cm, using the gravimetric method. Climatic data during the test were taken from a meteorological station located 1,500 m from the experimental area. The climatology was typical of the months in which the study was conducted (January-March) and only three precipitations (60 mm) were recorded. Abaxial gs were measured at different times of day and similar leaves evaluated the current osmotic potential (ΨOs Act.) and the osmotic potential at maximum saturation (ΨOs Sat). Soil moisture values were almost always higher or equal in the INCA-17 block than in the Amalia variety. The gs highest values were obtained at 11:00 am and 36 DAT in INCA-17 plants and the smaller ones at 14:00 hours at 49 DAT in both varieties. As for ΨOs Act, the most negative values corresponded to Amalia variety and reached 49 DAT values of -1.1 MPa. The Pearson correlation showed that the variables that correlated most with the gs in the morning hours were soil moisture, daily solar radiation (RSD according its acronymsin) and daily evaporation, and in the afternoon were the maximum values and average temperatures.

Key words: soil moisture, plant water relations, drought, tomato

RESUMEN. Se estudió el comportamiento de la conductancia estomática (gs) en plantas de las variedades de tomate INCA-17 y Amalia, cultivadas en condiciones de campo. Se realizaron perfiles de humedad a dos profundidades de 0–15 cm y de 15-30 cm, mediante el método gravimétrico. Los datos climáticos durante el ensayo se tomaron de una estación meteorológica ubicada a 1 500 m del área experimental. La climatología fue típica de los meses en que se realizó el estudio (enero-marzo) y solamente se registraron tres precipitaciones (60 mm). La gs abaxial se midió en diferentes horas del día y en hojas similares se evaluó el potencial osmótico actual (ΨOs Act.) y el potencial osmótico a máxima saturación (ΨOs Sat.). Los valores de humedad del suelo fueron casi siempre superiores o iguales en el bloque INCA-17 que en el correspondiente a la variedad Amalia. Los valores mayores de gs se obtuvieron a las 11:00 am y a los 36 DDT en plantas de Inca-17 y los menores a las 14:00 horas a los 49 DDT en ambas variedades. En cuanto al ΨOs Act., los valores más negativos correspondieron a las plantas de la variedad Amalia y alcanzó a los 49 DDT valores de -1,1 MPa. La correlación de Pearson realizada evidenció que las variables que más correlacionaron con la gs en horas de la mañana fueron la humedad del suelo, la radiación solar diaria (RSD) y evaporación diaria y en la tarde fueron los valores de las temperaturas máximas y medias.

Palabras clave: humedad del suelo, relaciones agua planta, sequía, tomate

INTRODUCTION

Drought is one of the most important abiotic stresses that limits crop productivity worldwide (1). Its incidence is expected to increase in frequency and intensity (2, 3) in some regions, due to the effects of climate change (4). This could have profound implications for countries in the regions affected in their socio-economic systems and in the tropical regions, where many developing countries are located and where poverty and malnutrition are already serious problems (5).

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Different environmental conditions can cause a water deficit in plants. Not only periods of low or no rainfall, also the presence of high concentrations of salts in the soil or low temperatures induce water deficiency (6, 7).

Globally in many agricultural areas, water scarcity significantly limits plant growth and productivity. Therefore, improving its efficient use is a fundamental priority, as it is an important feature for plant breeding.

Plant strategies to face with water scarcity imply a complex set of water and carbon traits. These features show strong interactions that may be relevant to different levels of organization and time scales (8). At the short scale of time and at the level of tissues and organs among the processes involved, the stomatal behavior is included (8).

To withstand drought stress, plants close their stomata to ensure turgidity and maintain cellular metabolism. As these close, the photosynthetic rate is reduced, plants must constantly adjust their stomatal conductance to allow sufficient CO_2 input and avoid unnecessary water losses during stress. Therefore, the plants must permanently feel the water deficit (9). Most crops, including tomato (*Solanum lycopersium* L.) are sensitive to water stress at different stages of development, from germination to fruit setting (10). As water is one of the most important environmental factors affecting fruit growth and tomato crop production, irrigation scheduling is crucial to increase yields and harvest quality (11).

On the other hand, inadequate exploitation of irrigation techniques causes losses and causes irreparable damages to the environment such as salinization of soils, contamination of aquifers, or degradation of the best land, which are usually under irrigation (12).

Although plant growth is controlled by a multitude of physiological, biochemical and molecular processes, photosynthesis is a key phenomenon, which contributes substantially to its growth and development (13); therefore, the study of the internal state and flow water in plants is important for understanding their adaptation to unfavorable environments and stomata are of vital importance to that function. They regulate the exchange of gas mainly of CO_2 and water vapor with the environment allowing the plants to optimize and balance the photosynthetic performance with the availability and water use (14).

In Cuba, there is not much information available on tomato cultivation in field conditions of physiological processes such as gas exchange and even less under limited water supply conditions.

The behavior of the plants under field conditions is almost always different to those grown under controlled conditions (growth chambers) due to a variety of factors, among which it can point out: higher evaporative demand and, therefore, high transpiration rate; soils with different hydraulic conductivities to the substrates used in the laboratory; environmental conditions that fluctuate constantly in a scale of time that goes from minutes to days (15).

Based on the above, the work aims to study the behavior of the stomatal conductance of two cuban tomato varieties under field conditions and with limited irrigation.

MATERIALS AND METHODS

The work was carried out in field conditions, in the Department of Agricultural Services of the National Institute of Agricultural Sciences. The species studied was *Solanum lycopersicon*, varieties "INCA 17" and "Amalia". For the execution of the work, two areas of approximately 1 000 m^2 each were selected with a 10 m spacing of a compacted Red Ferralitic soil (16).

In each previously identified block, an agrochemical sampling composed of five samples in diagonal up to 25 cm depth was carried out in order to know the fertility variations present in the experimental area. The soil analysis data were processed statistically by a simple classification ANOVA for each of the determined elements and the results are presented in Table I, where it was evidenced that the fertility was homogeneous in both blocks, with no differences detected statistically significant in any of the analyzed variables. In this way, a sample design was established, which is detailed as follows:

The postures of the two tomato varieties were planted in their corresponding blocks with a planting frame of 1,40 x 0,30 m. The two plots consisted of 20 rows of 40 m long each.

In the first 10 days after transplantation, three irrigations of 250 m^3 ha^{-1} were performed using a sprinkler system and at 56 days after transplantation (DAT), the plot cultivated with the INCA 17 variety received an additional irrigation of 250 m^3 ha^{-1} which was due to a specific study of the flowering of this variety. All cultural work was done equally on both plots. From the 36 DAT, different evaluations were carried out on the plants of the two varieties.

Table I. Chemical characteristics of Soil in Experimental Area

Block	Depth (cm)	C mol Kg^{-1} K changeable	Ca changeable	Mg changeable	Assim P. mg Kg^{-1}	O.M %	P H H_2O
I INCA 17	0 - 25	0,36	9,16	1,00	491, 20	2,01	6,86
II Amalia	0 - 25	0,36	9,16	1,00	487,74	1,98	6,88
E. s. X		0,01 ns	0,37 ns	0,10 ns	5,72 ns	0,07 ns	0,09 ns
C. V. (%)		8,91	9,12	12,77	2,61	7,32	2,98

In each plot three sampling areas were selected in order to know the soil moisture dynamics. Moisture profiles were made at two depths of 0-15 and 15-30 cm. For the extraction and management of the soil samples, a screwdriver auger and dampened aluminum capsules in each plot three sampling areas were selected in order to know the soil moisture dynamics. An auger ringlet and capsules moisture (weighing bottle) duly tared aluminum was used for the extraction and management of soil samples. The samples were processed by the gravimetric method with a drying time in a forced-draft oven of 20 hours at 110 ºC were used. Data were expressed as percentage of dry soil moisture and field capacity (C.c.) measurements were performed at 36, 42, 49, 57, 63, 70 and 77 days after transplantation.

Climatic data of minimum temperature °C (T. Min.), Maximum temperature ºC (T. Max.), Average temperature °C (T. Med.), Daily solar radiation in MJ m^{-2} day^{-1} (RSD), rain in mm and evaporation in mm were taken daily from a meteorological station located 1,500 m from the experimental area and they are expressed as averages by tens.

Stomatal conductance (gs) was measured at 10:00, 11:00, 12:00, 13:00, 14:00 and 15:00 hours on 10 plants for each variety in leaves of the upper third well exposed to the sun and using a diffusion porometer (Delta-T DevicesType AP4). Evaluations were performed at 36, 49, 63 and 77 DAT.

Similar papers evaluated the current osmotic potential (ΨOs Act.) And the osmotic potential at maximum saturation (ΨOs Sat).

For ΨOs Act, the leaves were covered with foil and frozen in liquid nitrogen. For the determination of ΨOs Sat., the selected leaves were placed in hydration chambers with distilled water, in the dark and at 6 to 8 °C for 24 hours. Immediately thereafter they were wrapped with foil for freezing in liquid nitrogen and stored at -20 °C.

Subsequently all the samples were thawed at room temperature and centrifugation (1 minute at 3000 rpm) obtained the cell juice of the leaves. From 100 mL aliquots, the ΨOs Act and ΨOs Sat., were determined from leaves with a VAPRO 5520 vapor pressure osmometer. For these evaluations five replicates were performed for each treatment.

All evaluations were performed at 36, 42, 49, 57, 63, 70 and 77 days after transplantation.

For the data processing, the comparison of means, and the calculation of the Confidence Intervals of the means were used the statistical program SPSS 10.0 for Windows. The results were plotted using the SIGMA PLOT 10.0. In addition, with the mean values of all variables and stomatal conductance in the different hours in which it was measured, a Pearson correlation was performed.

RESULTS AND DISCUSSION

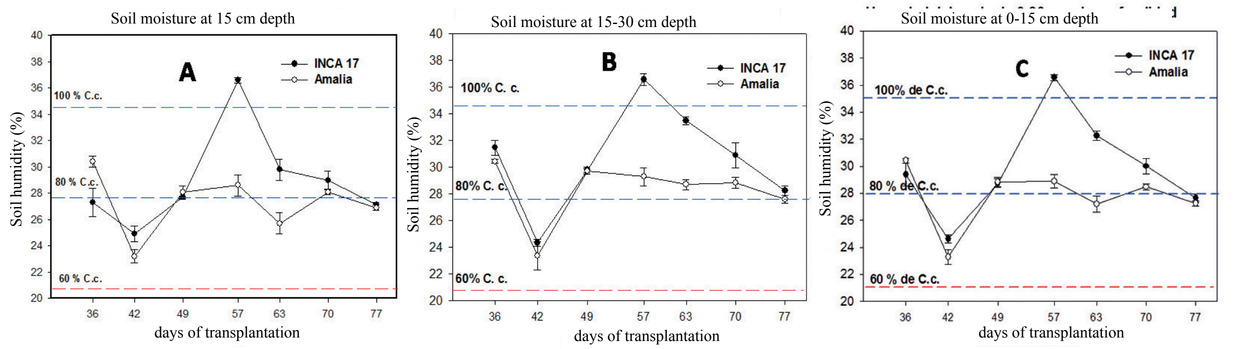
In Figure 1, the percentage values of soil moisture are presented for depths of 0-15 cm, 15-30 cm, as well as for the 0-30 cm profile. Statistical differences were observed in the first two samples; At 36 DAT moisture was greater than 88 % of field capacity (C.c.) in the block cultivated with the Amalia variety and lower in the INCA-17 variety (80 % of the C.c.). At 42 DAT soil moisture declined about 70 % of the C.c. In both blocks and the highest percentage of moisture corresponded to the block cultivated with INCA-17.

From the 57 DAT and up to 70 DAT, soil moisture at this depth was higher in the block of the INCA-17 variety, while at 77 DAT the values in both blocks were very similar and very close to 80 % of the C.c.

At the depth of 15-30 cm (Figure 1B), only statistical differences were found in soil moisture percentages at 57, 63 and 70 DAT in favor of the INCA-17 block due to the additional irrigation received. In the average profile 0-30 cm (Figure 1C) the behavior was very similar to that shown in Figure 1B.

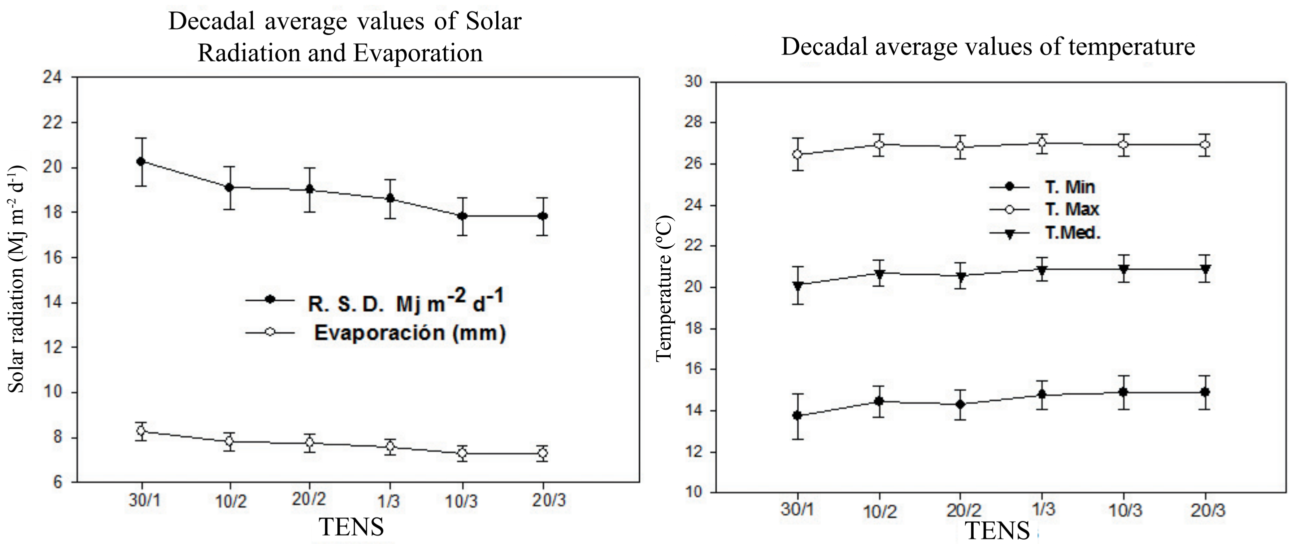
In general, it can be stated that the soil moisture values were almost always higher or equal in the INCA-17 block than in the Amalia variety.

The meteorological data in the period of the experiment are shown in Figures 2A and B, in 2A, the average decadal values of daily solar radiation (RSD) and evaporation (Ev) are presented, where it can be seen that the RSD values were around 21 Mj m^{-2} d^{-1} at the beginning of the experiment and around 18 Mj m^{-2} d^{-1} at the end, whereas the values of Ev at the beginning were around 9 mm and at the end about 7 mm.



The bars on the midpoints indicate the confidence interval of the means α = 0,5

Figure 1. Percentage values of soil moisture at 15 cm depth (A), 30 cm (B) and in the profile from 0 to 30 cm (C), measurements taken at 36, 42, 49, 57, 63, 70 and 77 DAT



The values of the minimum temperatures and the means were parallel to the maximums. Minimum ranged between 13 and 14,8 ºC.
During the period only three rain events (60 mm)
The bars on the midpoints indicate the confidence interval of the means α = 0,5

Figure 2. Ten-year average values of R.S.D. And evaporation (A) and maximum, minimum and average temperatures (B)

On the other hand, in Figure 2B, the temperatures in general varied little, the maximums were like decadal average between 26,4 and 26,9 ºC.

The stomatal conductance (gs) of the two varieties measured at 10:00, 11:00, 12:00, 13:00, 14:00 and 15:00 hours at 36, 49, 63 and 77 DAT are shown in Tables II and III, respectively, where it was found that the highest values of gs occurred at 11:00 am and at 36 DAT, with statistical differences din favor of the INCA-17 plants (Table II) and the lowest values of this variable were presented at 2:00 p.m. in the 49 DATs without statistical differences between the two varieties.

At the physiological level, stomatal closure constitutes a fundamental mechanism of tolerance to water stress, as these are responsible for the greater loss of water in the plants (17). In this sense, it would be more logical to expect that the highest values of gs in INCA-17 would be reached at 63 DAT when soil moisture was around 90 % of C.c.; on the contrary, in Amalia the lowest values had to be presented at 63, or at 77 DAT in both varieties, due to the lower values of soil moisture.

In this regard, other authors (18, 19) working with different models of photosynthesis and stomatal conductance associated with soil moisture have pointed out that no method completely replicates the observed response of stomata to soil water stress and there are doubts about the way In which the stress of soil moisture works when it comes to explaining the physical and physiological transport of water through the hydraulic-soil-plant-atmosphere continuum (14, 20, 21).

Table II. Mean values of stomatal conductance of the INCA-17 and Amalia varieties at 10, 11 and 12 hours of the day and at 36, 49, 63 and 77 DAT

DAT	10:00 am		11:00 am		12:00 m	
	INCA -17	Amalia	INCA -17	Amalia	INCA -17	Amalia
36	166±5	185±5	308±13	243±9	83±1	72±2
49	188±15	186±5	93±3	80±4	66±2	59±2
63	118±4	129±3	102±5	95±4	65±1	60±1
77	87±2	122±3	151±9	129±56	65±4	67±3

Values are the mean of 10 replicates ± the confidence interval (α = 0,5)

Table III. Mean values of stomatal conductance of the INCA-17 and Amalia varieties at 13, 14 and 15 hours of the day and at 36, 49, 63 and 77 DAT

DAT	13:00 pm		14:00 pm		15:00 pm	
	INCA -17	Amalia	INCA -17	Amalia	INCA -17	Amalia
36	87±4	96±4	76±4	78±3	99±3	81±3
49	78±3	65±1	61±1	59±3	83±2	65±2
63	76±5	104±5	123±5	106±4	107±2	116±6
77	136±9	105±6	83±2	78±3	97±3	106±3

Values are the mean of 10 replicates ± the confidence interval (α = 0,5)

It should be noted that, in general, the highest values of gs measured at 10:00 am corresponded to plants of the Amalia variety, except for the 49 DATs that were slightly lower than those of the INCA-17 plants. However, the values of gs measured at 11:00 and 12:00 hours were almost always similar or higher in INCA-17.

In the cultivation of cowpea (*Vigna unguiculata* (L.) (Walp.), it has been reported that stomatal closure as a result of the decrease in soil moisture content is an indicator of water stress and this varies with genotype (22).

The osmotic potential of the leaves is an important component of the water relations of the plants (23), it makes a negative contribution to the leaf water potential due to the concentration of solutes.

In Figure 3A and 3B, the dynamics of ΨOs Act., and ΨOs Sat., respectively, were found where the less negative values of ΨOs Act. (Figure 3A) corresponding to 36, 49, 57, 70 and 77 DAT were characteristic of the plants of the Amalia variety with statistical differences compared to those of the INCA-17 variety, indicating that in the latter the solutes concentration was higher, mainly due to dehydration, 49 DAT this indicator in the INCA-17 plants reached values close to -1,1 MPa.

On the other hand, in Figure 3B, variations in the values of ΨOs Sat., mainly in plants of the variety INCA-17 were different than expected, since these had equal or higher values of ΨOs Sat., to the rest of plants of the Amalia variety at 42, 49, 57, 63 and 70 DAT and only lower values at 36 and 77 DAT with statistical differences.

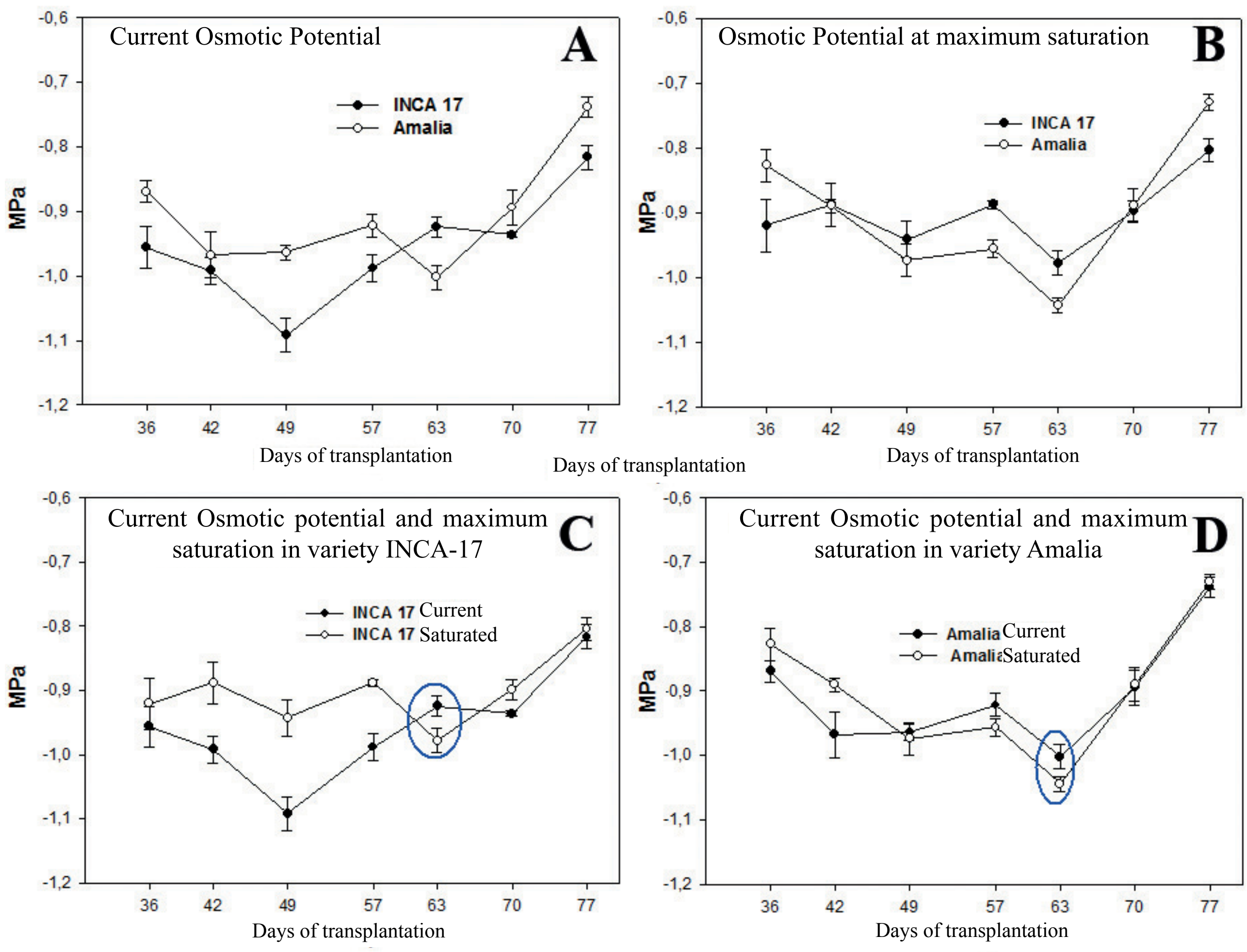
This behavior is possibly associated with the plants of the Amalia variety exhibiting greater stomatal control of water loss through transpiration. This stomatic control or regulation of the gas is a phenomenon of great importance for plants, because it allows to avoid dehydration and to ensure the entry of CO_2.

Other studies indicate (24) that stomatal closure in response to stressful conditions of drought and salinity generally occurs due to a decrease in foliar turgor or atmospheric pressure deficit coupled with chemical signals generated by the roots. Therefore, the decrease of the photosynthetic rate under stress conditions (salinity, drought and temperatures) is usually attributed to the stopping of the mesophile conductance and stomatal closure in moderate and severe stress situations.

The drought effects on photosynthesis are directly attributed to stomatal limitations by diffusion of gases, which ultimately alters the photosynthetic process and the metabolism of the mesophyll.

As for the comparison of ΨOs Act., and ΨOs Act in INCA-17 (Figure 3C), the values of ΨOs Act., At 42, 49, 57 and 70 DAT were more negative than ΨOs Sat., with statistical differences between the two, these values were equal to 36 and 77 DAT and only to 63 DAT the ΨOs. Sat., it was smaller.

In the plants of the Amalia variety (Figure 3D) only at 42 DAT the ΨOs Act., was inferior to the ΨOs Act. It is highlighted the fact that at 63 DAT the values of ΨOs Sat were more negative than those of ΨOs Act, due to a higher concentration of solutes, suggesting the possible occurrence of a slight process of osmotic adjustment in the leaves of both varieties. Changes in water supply are reflected in passive and reversible or active and irreversible variations of the ΨOs Act of vacuolar fluid.



The bars on the midpoints indicate the confidence interval of the means α = 0,5

Figure 3. Dynamics of ΨOs Act (A) and ΨOs Sat (B). Comparison of both ΨOs Act and ΨOs Sat in INCA-17 (C) and in Amalia (D)

These variations in plants under intense radiation range from 0,2 to 0,6 MPa between the maximum value (half day) and the minimum value (sunrise) and they are due to a transient imbalance between the absorption and the loss of water. Under an unfavorable water balance with an internal water imbalance, a defense mechanism is the 'osmotic adjustment', by decreasing the ΨOs Act to maintain the turgity.

The osmotic adjustment consists in a reduction of the water potential in the plant tissues, which allows the entrance of water and prevents the decrease in the turgor or in the photosynthetic activity; Is originated through the biosynthesis of low molecular weight organic osmolytes and by the accumulation of ions, especially K^+ (25).

This process of osmotic adjustment is an important mechanism for the maintenance of water consumption and cellular turgidity in conditions of water stress (26).

Tables IV and V show the results of the Pearson correlations performed with the values of gs measured at different hours of the day versus values of soil moisture, osmotic potentials and climatic variables, where it was found that the gs measured at 10:00 am in the INCA-17 plants had a negative correlation with the ΨOs Act, while the Amalia plants showed positive correlations with soil moisture values. With the measurements at 11:00 am gs in both varieties had no correlation with any of the variables analyzed. At 12.00 m, the gas measurements of the INCA-17 plants showed positive correlations with the values of soil moisture and negative with daily solar radiation (RDS) and daily evaporation.

In the case of the gs of the Amalia variety plants, only showed negative correlations with RDS and daily evaporation.

Table IV. Pearson correlation between gs (mmol H_2O m^{-2} s^{-1})

Varieties	INCA-17	Amalia	INCA-17	Amalia	INCA-17	Amalia
Variables	gs (10:00 am)		gs (11:00 am)		gs (12:00 m)	
H. soil 0-15 cm. (%)	0, 33 n.s.	0,82 n.s.	0,01 n.s.	0,65 n.s.	0,92 **	0,31n.s.
H. soil 15-30 cm. (%)	0,76 n.s.	0.94 *	0,36 n.s.	0,35 n.s.	0,77*	0,05 n.s.
H. soil 0-30 cm (%)	-0,77 n.s.	0,96 **	0,18 n.s.	0,54 n.s.	0,88 **	0,15 n.s.
ΨOs Act. (MPa)	-0,95 *	-0,30 n.s.	0,19 n.s.	0,42 n.s.	-0,07 n.s.	0,18 n.s.
ΨOs Sat. (MPa)	-0,56 n.s.	-0,14 n.s.	0,11 n.s.	0,48 n.s.	0,06 n.s.	0,30 n.s.
Min temperature. (ºC)	0,40 n.s.	0,63 n.s.	0,62 n.s.	0,53 n.s.	0,53 n.s.	0,54 n.s.
Max temperature. (ºC)	0,35 n.s.	0,56 n.s.	0,32 n.s.	0,25 n.s.	0,18 n.s.	0,26 n.s.
Mean temperature. (ºC)	0,39 n.s.	0,62 n.s.	0,51 n.s.	0,42 n.s.	0,39 n.s.	0,42 n.s.
R. S. D. (Mj m^{-2} $days^{-1}$)	-0,75 n.s.	-0,86 n.s.	-0,52 n.s.	0,36 n.s.	-0,94**	-0,86 **
Evaporation (mm)	-0,76 n.s.	-0,86 n.s.	-0,50 n.s.	-0,34 n.s.	-0,93**	-0,86 **

Measured at 10:00 AM, 11:00 AM and 12:00 AM, with variables, soil moisture at different depths, osmotic potential values and climatic variables
(-) negative correlation * Significance at 5% and * * significance at 1 %

Table V. Pearson's correlation between the stomatal conductance of the INCA-17 and Amalia varieties measured at 1:00 p.m., 2:00 p.m. and 3:00 p.m., with percentage values of soil moisture at different depths, osmotic potential values and climatic variables

Varieties	INCA-17	Amalia	INCA-17	Amalia	INCA-17	Amalia
Variables	13:00 pm		14:00 pm		15:00 pm	
H. soil 0-15 cm. (%)	0,81 **	n.s.	0,16 n.s.	0,11 n.s.	-0,15 n.s.	0,24 n.s.
H. soil 15-30 cm. (%)	0,70 *	n.s.	0,25 n.s.	0,35 n.s.	0,08 n.s.	0,50 n.s.
H. soil 0-30 cm (%)	0,79 **	n.s.	0,19 n.s.	0,17 n.s.	-0,05 n.s.	0,30 n.s.
ΨOs Act. (MPa)	0,18 n.s.	n.s.	0,73*	0,18 n.s.	0,54 n.s.	-0,03 n.s.
ΨOs Sat. (MPa)	0,47 n.s.	n. s.	-0,65 n.s.	0,33 n.s.	-0,70 n.s.	-0,42 n.s.
Min temperature. (ºC)	0,34 n.s.	n. s.	-0,73 *	0,63 n.s.	-0,52 n.s.	-0,60 n. s.
Max temperature. (ºC)	0,19 n.s.	n. s.	-0,93 **	-0,88 **	0,66 n.s.	-0,80 *
Temperatura Mean. (ºC)	0,28 n.s.	n.s.	-0,83 **	-0,75 *	-0,59 n.s.	-0,70 n.s.
R. S. D. (Mj m^{-2} day^{-1})	-0,36 n.s.	n.s.	0,29 n.s.	0,19 n.s.	0,10 n.s.	-0,03 n.s.
Evaporation (mm)	-0,35 n.s.	n.s.	0,28 n.s.	0,19 n.s.	0,09 n.s.	-0,04 n.s.

(-) negative correlation * Significance at 5 % and * * significance at 1 %

When analyzing the correlations in the afternoon (Table V), it was found that at 13:00 hours, gs in the INCA-17 variety showed positive correlations with soil moisture, while in the Amalia plants they did not present correlation. At 14:00 hours INCA-17 showed a positive correlation of its gs with the ΨOs Act., and negative correlations with the values of the temperatures, while the gs in Amalia showed negative correlations with the maximum and average temperatures. At 15 hours, only the plants of Amalia showed negative correlation of their gs with the values of maximum temperatures.

CONCLUSIONS

- By way of conclusion, it can be considered that the variables that correlated most with the gs of the plants of both varieties were in the morning the values of soil moisture, RSD and daily evaporation, while in hours of the afternoon, were the values of the temperatures, mainly the maximums and the means.
- These results show that the mechanisms involved in stomatal response to environmental variations are multiple and have quantitatively different, even sometimes conflicting, effects on stomatal conductance (15). Therefore, it is necessary to identify the mechanisms that make a greater contribution to gs in a given range of environmental conditions.

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