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Gas exchange in upland cotton cultivars under water deficit strategies

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Aiming to evaluate the gas exchange of upland cotton cultivars cultivated in the Brazilian semiarid, subject to water deficit periods on the phenological stages, an experiment was carried out at the Campina Grande Federal University, Pombal county campus, Paraíba State, Brazil, between June and December 2015. Treatments were formed from a split-plot arrangement, in which the plots were 6 water deficit periods (P) (P1 = No deficit, P2 = Deficit in the initial growth stage, P3 = Deficit in the flower bud stage, P4 = Deficit in the flower stage, P5 = Deficit in the boll stage and P6 = Deficit in the open boll stage) and the subplots, 2 upland cotton cultivars (C) (C1 = Brazil Seeds 286 and C2 = BRS 336), in randomized block design, with 4 replicates. Water deficits reduced the gas exchange of the upland cotton plants, mainly stomatal conductance, transpiration and photosynthesis. The cotton cultivars BRS 286 and BRS 336 presented similar behavior in the different water deficits applied on different phenological stages. Cotton was less tolerant to water deficits in the boll formation stage and more tolerant in the initial growth and flower bud stages.

Key words: *Gossypium hirsutum* L. r. *latifolium* H., water stress, physiology.

INTRODUCTION

Cotton is one of the most important socioeconomic products for Brazil. Besides being the most important natural source of fibers, it gives the country a privileged place in the international scene, as it is one of the five largest producers in the world, along with China, India, the United States and Pakistan (Abrapa, 2018).

Because of its C_3 metabolism, upland cotton highly demands light, but is considered inefficient on its absorption once it shows leaf senescence regarding to its phenology (Beltrão et al., 2011). In this sense, cotton crop in the Brazilian semiarid zones has a favorable factor, as, according to Silva et al. (2010), the duration of the mean solar day that is approximately 12 h, since the region is near to the Equator line.

In the semiarid region of the Northeast of Brazil, cotton is frequently subjected to soil water deficit in different

durations and intensities, mainly because of the scarcity or lack of rainfall in this region. Ashraf (2010) considers water deficit to be one of the main environmental constraints, which contributes to the decrease in crop yield and food security around the world.

The occurrence of water deficit is visible at any phenological stage of the plant and it may vary according to the severity and duration of the stress (Farooq et al., 2009), which includes changes in the photosynthetic rate, transpiration rate and in the stomatal conductance (Furlan et al., 2012).

Studies about water relations in plants and the interactions caused by water deficit on physiological processes are of fundamental importance, as well as the knowledge on the variation of the water consumed by a crop in its different stages of development. Such information allows the description of the physiological behavior and its consequences (Peixoto et al., 2006).

Several physiological indexes are related to the use of water by plants. Among them, photosynthesis and stomatal conductance stand out, as osmotic adjustment, such as stomatal closure, allows plants to escape dehydration and loss of turgor through the maintenance of the water content in the cells (Roza, 2010).

One of the ways to verify if the crop is under suitable conditions of cultivation is related to plant gas exchange, as, according to Taiz and Zeiger (2013), the plant under stress tends to reduce its cellular water potential, closing the stomata and reducing the formation of photoassimilates.

As gas exchanges are directly linked to the availability of water (Taiz and Zeiger, 2013), irrigation is needed to meet the water needs of the crop for a successful production; on the other hand, techniques that allow the maintenance of soil water can also be used, as they allow the plants to complete their production cycle (Guimarães et al., 1996).

However, the use of irrigation, while presenting great advantages to the agricultural production system, can cause environmental problems and increase the production cost, which is why it is important to increase the efficient use of water in irrigated crops, especially in arid and semiarid regions, where water availability is limited.

It is also known that some crops have economically viable yields even under soil water deficit, while others are sensitive to relatively low levels of scarcity. This difference is due to factors related to the root system, in particular to factors that influence growth, such as the physical characteristics of the soil, the genetic characteristics of plants and the management of irrigation systems (Reichardt and Timm, 2004).

When subjected to water deficit, plants present different responses and some are tolerant, even if they have to modify their morphophysiological and biochemical characteristics, while others, considered not tolerant, develop stress symptoms (Chakraborty et al., 2015).

Therefore, the efficiency of water use for irrigated production systems need to be optimized, especially in the cotton crop, as it is a species of great economic and social importance, so, it is important to identify adequate strategies to optimize the use of water.

Based on these reports, the objective of this study was to evaluate the gas exchange of upland cotton cultivars cultivated in the Brazilian semiarid, subjected to water deficit periods on the phenological stages, in order to relate the rational use of water to sustainable crop production in the semiarid region of Paraíba State, Brazil.

MATERIALS AND METHODS

The experiment was conducted under field conditions between June and December 2015 in the experimental area of the Center for Agricultural Science and Technology, of the Campina Grande Federal University, Campus of Pombal county, Paraíba State, Brazil, located in the following geographic coordinates; 06°47'52"S, 37°48'10"W and 175 m above mean sea level.

The predominant climate of the region is hot semiarid (the BSh type), according to Köppen climate classification. The soil of the experimental area was classified as Fluvic Neo-soil (Santos et al., 2013), loamy sand texture (80% sand, 5.96% clay and 14.51% silt) and water tension curve of 15.49% (at 0.1 atm – Field Capacity - FC), 4.63% (at 15.0 atm – Permanent Wilting Point - PWP) with available water content (AWC) of 6.63% at the depth of 0 to 40 cm.

Fertilization was carried out according to the technical recommendations for the crop (Cavalcanti, 2008), based on the analysis of soil fertility (Table 1), in the foundation, by the application of 30 kg ha^{-1} of N, 40 kg ha^{-1} of P_2O_5 and 10 kg ha^{-1} of K_2O and in 2 covers, with the application of 30 kg ha^{-1} of N and 5 kg ha^{-1} of K_2O. Liming was not needed.

Upland cotton cultivars were planted in single rows, spaced 1.0 m between rows × 0.10 m among plants.

The water used in the irrigation presented C_2S_1 salinity (low alkali and medium salinity hazard, an electric conductivity - EC of 0.315 dSm^{-1}) and low sodium adsorption ratio (SAR = 1.78). Such water can be used for irrigation whenever there is a moderate degree of leaching and special care in the preparation of the soil.

Water was applied by a localized irrigation system, with drip tapes and emitters spaced 0.10 m apart. Each treatment consisted of a lateral line, spaced from the other lines by 1 m, with 6 m of length, each.

Subsequently, after installation of the irrigation system and beginning of the experiment, a water distribution test was carried out in the field. Through this, the mean precipitation applied was determined as 8.86 mm h^{-1} and application efficiency (Ae) as 91%, according to Bernardo et al. (2008).

Irrigations were carried out daily, always in the morning, based on the availability of soil water (AWC) to plants. The replacement water volume was calculated considering the water lost by the crop evapotranspiration, which is represented as the difference between the soil water content (SWC) in the field capacity (FC) and the current mean SWC measured in the depths of 0.10, 0.20, 0.30 and 0.40 m, which were measured before irrigations. The current SWC was determined by the time-domain reflectometry (TDR) method, using a Delta-T-PR2 probe introduced through access pipes installed in each treatment.

With the data of the current SWC, using an Excel spreadsheet, in which the daily values of the current SWC and the AWC to plants were recorded, the depth for the replacement of water and the time of irrigation were calculated for the treatments, which were the basis for the determination of the Net and Gross Irrigation Depth

Table 1. Chemical characteristics of the soil of the experimental area at different depths. Pombal county, Paraíba state, Brazil. 2015.

Depth (cm)	pH (water)	OM (%)	P (mg 100 g^{-1})	Na$^+$	K$^+$	Ca^{2+}	Mg^{2+}
0-20	6.79	1.16	51.5	0.14	0.42	4.28	1.40
20-40	6.94	0.78	49.0	0.15	0.27	4.03	1.89

pH = hidrogenionic potential; OM = organic matter.
Source: Irrigation and Salinity Laboratory, UFCG, Campina Grande county, Paraíba State, Brazil.

Table 2. Detail of the deficit treatments. Pombal county, Paraíba state, Brazil. 2015.

Treatment	Period of application of the deficit	Beginning of the deficit	Ending of the deficit	Total irrigation depth applied (La - mm)
No deficit (P1)	-	-	-	732.41
Deficit in the initial growth stage (P2)	22/Jul to 04/Aug	29 DAG	43 DAG	686.65
Deficit in the flower bud stage (P3)	03/Aug to 16/Aug	40 DAG	54 DAG	608.39
Deficit in the flower stage (P4)	18/Aug to 31/Aug	54 DAG	68 DAG	603.53
Deficit in the boll stage (P5)	26/Aug to 08/Sep	62 DAG	76 DAG	610.85
Deficit in the open boll stage (P6)	03/Oct to 16/Oct	100 DAG	114 DAG	649.67

(P1), …,(P6) = treatments designation; DAG = days after germination.

(NID and GID), according to Mantovani et al. (2009).

Treatments were formed from a split-plot arrangement, in which the plots were 6 water deficit periods (P) (P1 = No deficit, P2 = Deficit in the initial growth stage, P3 = Deficit in the flower bud stage, P4 = Deficit in the flower stage, P5 = Deficit in the boll stage and P6 = Deficit in the open boll stage) and, the subplots, 2 upland cotton cultivars (C) (C1 = Brazil Seeds 286 and C2 = BRS 336), in randomized block design, with 4 replicates, amounting to 48 experimental subplots.

Each period of water deficit consisted of 14 days without irrigation in the predetermined phenological stage, according to Table 2. After this period, the plants had normal irrigation until the end of the cycle. The total irrigation depth applied for each treatment is also presented in Table 2. The necessary phytosanitary treatments were carried out when the first injuries and symptoms of pests and diseases appeared, as well as crop treatments for weed control.

The gas exchanges evaluations were performed at 29, 40, 54, 62 and 100 days after germination (DAG) from measuring stomatal conductance (gs) (mol H_2O m^{-2} s^{-1}), transpiration (E) (mmol H_2O m^{-2} s^{-1}), net photosynthesis (A) (μmol CO_2 m^{-2} s^{-1}) and internal CO_2 concentration (Ci) (μmol CO_2 mol^{-1}). With these data, the instantaneous water-use efficiency (iWUE) (A/E) [(μmol CO_2 m^{-2} s^{-1}) / (mmol H_2O m^{-2} s^{-1})$^{-1}$] and the instantaneous carboxylation efficiency (iCE) (A/Ci) [(μmol CO_2 m^{-2} s^{-1}) / (μmol CO_2 mol^{-1})$^{-1}$] were estimated, following Konrad et al. (2005) and Magalhães Filho et al. (2008). These evaluations were performed with a plant gas exchange (model LCpro – SD, ADC Bioscientific, UK), containing an infrared gas analyzer (IRGA). The readings were performed on the third fully expanded leaf, conducted under natural conditions of air temperature, CO_2 concentration and using an artificial radiation source of 1200 μmol m^{-2} s^{-1}.

The obtained data were subjected to analysis of variance through the F-test and the means of the factor levels, both qualitative, were compared by the Tukey test at 5% of probability using the statistical program SISVAR (Ferreira, 2011).

RESULTS AND DISCUSSION

Because the higher concentration of cotton roots is in the 0.0 to 0.40 m depth layer, according to Amaral and Silva (2008), the soil moisture profiles were evaluated in this layer, during 126 days, in all treatments of water deficit periods (P1, …, P6) (Figure 1), comparing them to the water content in the FC and PWP averages of soil of experimental area.

It can be observed that soil moisture in all treatments of each water deficit period was very
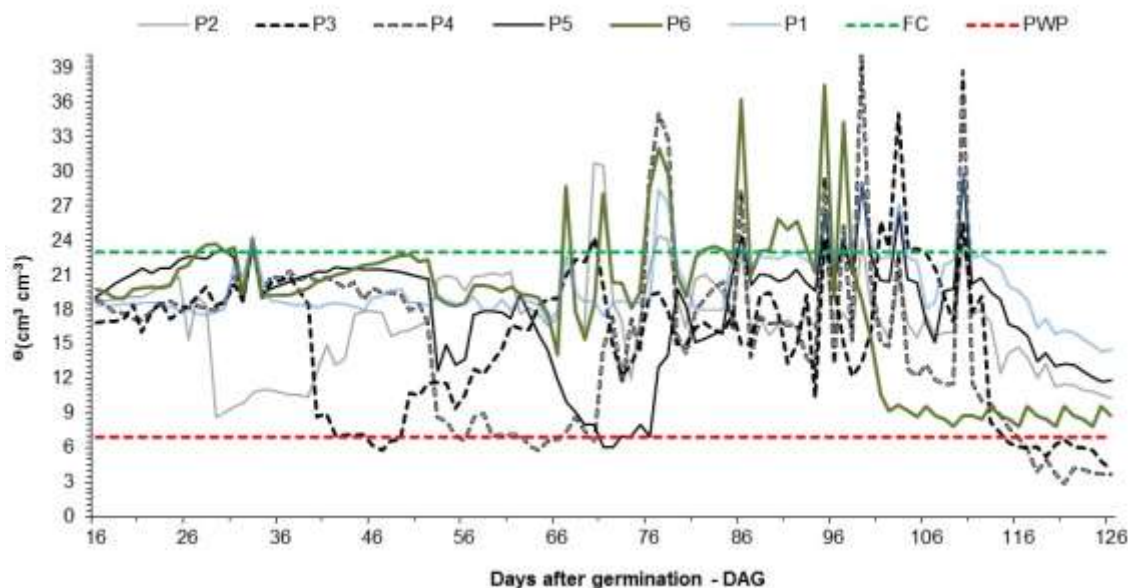
Figure 1. Variation of soil water content on the different water deficit treatments along experimental period. Pombal county, Paraíba state, Brazil. 2015.

close to the PWP, which increased during the period of application of the deficit and remained in approximately 50% of the AWC after this application. The deficit treatment applied in the open boll stage presented the same behavior of the irrigated treatment until a little before the application of the deficit period (Figure 1).

According to Sun et al. (2015), tolerance to water stress depends on the plant growth stage and, when water deficit occurs at critical stages, such as the reproductive stage, plant growth and development may be affected. Thus, it is very likely that the metabolic and physiological functions of the plants have been severely affected in this study.

Based on the analysis of variance, a significant difference could be seen for water deficit periods (P) in gs and E (except for 54 DAG, for E), A (at 29, 40, 54, 62 and 100 DAG), Ci (only at 29 and 40 DAG) and iCE (at 29 and 62 DAG). No statistical significance was observed for cultivar (C) and interaction (P × C) (Table 3).

In the comparison of means (Table 4) of gs, at 29, 40, 54, 62 and 100 DAG in the water deficit periods, the lowest mean values were found at 29 DAG in which the lowest value was observed in plants under P2 (0.16 mol H_2O m^{-2} s^{-1}); at 40 DAG, under P3 (0.15 mol H_2O m^{-2} s^{-1}); and at 54, 62 and 100 DAG under P4, P5 and P6, with mean values of 0.20, 0.12 and 0.13 mol H_2O m^{-2} s^{-1}, respectively.

In addition, there was a decrease in gs of 46.67% (P2), 48.28% (P3), 28.58% (P4), 60.00% (P5) and 38.10% (P6), in comparison with plants that were not subjected to stress (P1) (Table 4). These results corroborate Rocha and Távora (2013), who have found a significant effect of

water deficit on cowpea and stated that water restriction for 15 days in the vegetative stage reduced the plant gs.

According to Taiz and Zeiger (2013), gs is dependent on stomatal opening, which, among other factors, depends on the soil water availability. In this study, the decrease in gs (opening) was therefore due to the water stress to which the cotton plants were exposed and it is normal to expect lower values after the deficit period.

However, when determining the difference between the value observed in the plants under stress in the period with the values of of the plants that were not subjected to stress, the greatest decrease can be observed in plants subjected to stress at P5 (60%), which corresponds to the boll period (Table 4), when there is a high demand for water for fruit growth and this cause the plant to adapt by closing the stomata more effectively.

Influence of water deficit on gs has also been observed by Vasconcelos et al. (2018) who have studied cotton under water deficit after the second week of water suppression, however, as in this work, it was possible to observe the recovery of the plants after stress, which indicates their tolerance to stress.

It is probable that in the water deficit periods, the photosynthetic apparatus of the plants used strategies to minimize the effects of the deficit, following the same trend. According to Echer (2014), the stoma begins to close as a reaction to the decrease in leaf water potential, which decreases the rate of water loss.

As regard as the cultivar influence, the mean values of gs were 0.27, 0.26, 0.26, 0.26 and 0.19 mol. H_2O m^{-2}s^{-1} for cultivar BRS 286 and BRS 336, respectively (Table 4). Stomatal conductance determined under field conditions

Table 3. Summary of the analysis of variance for gas exchange variables at different evaluation ages of two upland cotton cultivars under different water deficit strategies in the phenological stages (Pombal county, Paraíba State, Brazil. 2015).

Variable	DAG	DF	MS (Deficit periods (P))	DF	MS (Cultivar (C))	DF	MS (P x C)	CV1 %	CV2 %	General mean
gs		5	0.0263^{**}	1	0.0001^{ns}	5	0.0015^{ns}	19.23	15.42	0.27
E		5	1.2008^{*}	1	0.0013^{ns}	5	0.0172^{ns}	10.34	9.59	2.70
A		5	114.7063^{**}	1	11.4270^{ns}	5	9.8188^{ns}	9.36	8.82	21.23
$iWUE$		5	1.9625^{ns}	1	0.9240^{ns}	5	1.5026^{ns}	14.54	9.44	7.59
Ci	29	5	4644.98^{**}	1	675.00^{ns}	5	640.90^{ns}	10.06	13.51	195.20
iCE		5	0.0012^{*}	1	0.0010^{ns}	5	0.0006^{ns}	17.26	16.06	0.10
gs		5	0.0268^{**}	1	0.0065^{ns}	5	0.0032^{ns}	20.57	16.09	0.26
E		5	2.4424^{*}	1	0.4800^{ns}	5	0.0493^{ns}	23.71	16.23	3.18
A		5	75.5322^{**}	1	42.3752^{ns}	5	5.9201^{ns}	16.98	13.58	22.09
$iWUE$		5	1.2570^{ns}	1	1.8881^{ns}	5	1.5025^{ns}	31.97	19.10	7.25
Ci	40	5	4650.18^{**}	1	63.02^{ns}	5	126.02^{ns}	8,32	9.47	202.93
iCE		5	0.0010^{ns}	1	0.0006^{ns}	5	0.0003^{ns}	21.93	21.84	0.11
gs		5	0.0139^{**}	1	0.000002^{ns}	5	0.0006^{ns}	18.01	12.97	0.25
E		5	0.9737^{ns}	1	0.0143^{ns}	5	0.0100^{ns}	26.68	9.17	3.35
A		5	25.9298^{**}	1	0.1376^{ns}	5	3.3243^{ns}	8.84	8.51	22.27
$iWUE$		5	0.7836^{ns}	1	1.0354^{ns}	5	0.1635^{ns}	21.21	11.75	6.94
Ci	54	5	1813.48^{ns}	1	667.52^{ns}	5	721.12^{ns}	18.03	9.16	181.56
iCE		5	0.0004^{ns}	1	0.00005^{ns}	5	0.0003^{ns}	20.63	14.61	0.12
gs		5	0.0411^{**}	1	0.0001^{ns}	5	0.0008^{ns}	23.76	15.64	0.26
E		5	4.8588^{**}	1	0.0645^{ns}	5	0.1973^{ns}	21.61	15.58	3.81
A		5	258.2148^{**}	1	17.5087^{ns}	5	24.7644^{ns}	15.22	18.27	21.08
$iWUE$		5	3.3935^{ns}	1	0.0792^{ns}	5	0.9592^{ns}	22.41	18.87	5.59
Ci	62	5	2102.23^{ns}	1	2.52^{ns}	5	910.37^{ns}	17.85	15.74	179.43
iCE		5	0.0062^{**}	1	0.0006^{ns}	5	0.0020^{ns}	22.45	31.30	0.12
gs		5	0.0064^{**}	1	0.00003^{ns}	5	0.0001^{ns}	9.91	7.10	0.19
E		5	0.8774^{**}	1	0.0760^{ns}	5	0.4822^{ns}	9.96	6.17	3.99
A		5	15.9181^{**}	1	7.8246^{ns}	5	0.7661^{ns}	10.07	7.06	14.60
$iWUE$		5	0.2357^{ns}	1	0.1354^{ns}	5	0.3589^{ns}	13.04	8.50	3.68
Ci	100	5	678.78^{ns}	1	126.75^{ns}	5	1855.90^{ns}	10.83	10.53	195.58
iCE		5	0.0003^{ns}	1	0.0005^{ns}	5	0.0004^{ns}	16.09	16.24	0.07

^{ns,**,*}: not significant and significant at $p \leq 0.01$ and $p \leq 0.05$; respectively (F-Test). DAG = days after germination; MS = Mean Squares; CV = coefficient of variation

Table 4. Mean values of stomatal conductance at different evaluation ages of two upland cotton cultivars under different water deficit strategies in the phenological stages (Pombal county, Paraíba State, Brazil. 2015).

Factor (Deficit periods)	Stomatal conductance (*gs*)				
	29 DAG	40 DAG	54 DAG	62 DAG	100 DAG
P1	0.30[a]	0.29[a]	0.28[a]	0.30[a]	0.21[a]
P2	0.16[b]	0.28[a]	0.29[a]	0.31[a]	0.20[a]
P3	0.30[a]	0.15[b]	0.21[b]	0.27[a]	0.21[a]
P4	0.28[a]	0.28[a]	0.20[b]	0.26[a]	0.20[a]
P5	0.31[a]	0.26[a]	0.29[a]	0.12[b]	0.19[a]
P6	0.29[a]	0.31[a]	0.27[a]	0.29[a]	0.13[b]
General mean	0.27	0.26	0.26	0.26	0.19
(Cultivars)					
BRS 286	0.27[a]	0.27[a]	0.26[a]	0.26[a]	0.19[a]
BRS 336	0.27[a]	0.25[a]	0.26[a]	0.25[a]	0.19[a]
General mean	0.27	0.26	0.26	0.26	0.19

Same letters in the column indicate no significant difference among among each factor level (Tukey, p<0.05).
DAG = days after germination.

Table 5. Mean values of transpiration at different evaluation ages of two upland cotton cultivars under different water deficit strategies in the phenological stages (Pombal county, Paraíba State, Brazil. 2015).

Factor (deficit periods)	Transpiration (*E*)				
	29 DAG	40 DAG	54 DAG	62 DAG	100 DAG
P1	2.87[a]	3.46[a]	3.66[a]	4.28[a]	4.25[a]
P2	2.00[b]	3.14[ab]	3.69[a]	4.34[a]	3.77[ab]
P3	2.96[a]	2.08[b]	3.19[a]	3.82[a]	4.18[a]
P4	2.89[a]	3.52[a]	2.76[a]	4.12[a]	4.17[a]
P5	3.04[a]	3.35[a]	3.49[a]	2.27[b]	4.14[a]
P6	2.95[a]	3.49[a]	3.31[a]	4.04[a]	3.41[b]
General mean	2.79	3.18	3.35	3.82	3.99
(Cultivars)					
BRS 286	2.79[a]	3.28[a]	3.33[a]	3.85[a]	4.03[a]
BRS 336	2.78[a]	3.08[a]	3.36[a]	3.78[a]	3.95[a]
General mean	2.79	3.18	3.35	3.82	3.99

Same letters in the column indicate no significant difference among each factor level (Tukey, p<0.05). DAG = days after germination.

is difficult to predict for many cultivars because of the environmental variations that occur during an evaluation procedure that may affect *gs* throughout the period (Echer, 2014).

Opposite results have been found by Soares (2016), who has studied the tolerance of colored cotton genotypes to saline stress in the different phenological stages and by Graciano et al. (2016), who have studied the gas exchange of peanut cultivars under soil water deficit, which, with the restriction of available soil water, had a significant decrease in gs in all cultivars studied.

Because of the partial stomatal closure, decreased *E* could be observed when water deficit was applied at 29 DAG in which the lowest value was observed in plants under P2 (2.00 mmol H_2O m^{-2} s^{-1}), at 40 DAG in P3 (2.08 mmol H_2O m^{-2} s^{-1}) and at 62 and 100 DAG under P5 and P6, with mean values of 2.27 and 3.41 mmol H_2O m^{-2} s^{-1}, respectively (Table 5).

There was a decrease in *E* of 30.31% (P2), 39.88% (P3), 23.77% (P4), 46.96% (P5) and 19.78% (P6) when compared to plants that did not undergo stress (P1) too (Table 5), following, in part, the results observed for gs, since soil water deficit induces stomatal resistance, decreasing the loss of water by transpiration, which may be related to the possible decrease in water potential as a consequence of the water deficit.

Table 6. Mean values of net photosynthesis at different evaluation ages of two upland cotton cultivars under different water deficit strategies in the phenological stages (Pombal county, Paraíba State, Brazil. 2015).

Factor (deficit periods)	Net photosynthesis (A)				
	29 DAG	40 DAG	54 DAG	62 DAG	100 DAG
P1	23.48[a]	23.80[a]	23.44[a]	25.26[a]	16.02[a]
P2	13.62[b]	22.52[a]	22.68[a]	23.32[a]	14.75[a]
P3	22.39[a]	15.93[b]	20.69[ab]	22.35[a]	15.36[a]
P4	21.65[a]	23.25[a]	19.43[b]	21.06[a]	14.49[a]
P5	23.23[a]	22.90[a]	23.60[a]	9.90[b]	15.04[a]
P6	23.00[a]	24.14[a]	23.80[a]	24.57[a]	11.93[b]
General mean	21.23	22.09	22.28	21.08	14.60
(Cultivars)					
BRS 286	21.72[a]	23.03[a]	22.33[a]	21.68[a]	15.00[a]
BRS 336	20.74[a]	21.15[a]	22.22[a]	20.47[a]	14.19[a]
General mean	21.23	22.09	22.28	21.08	14.60

Same letters in the column indicate no significant difference among each factor level (Tukey, $p < 0.05$). DAG = days after germination.

This corroborates Rocha and Távora (2013), who have stated that water restriction for 15 days in the vegetative stage decreased transpiration to levels significantly below those normally found in irrigated plants and this decrease, although significant, allowed the maintenance of the transpiration process and a recovery in the transpiration of cotton plants could be observed after the deficit period and return of irrigations. Corroborating with this research, Soares (2016) and Graciano et al. (2016) have also verified decreases in E as a function of treatments. The decrease in E may have been caused by the lack of water in the root zone of the plant, as well as by the low capacity of osmotic adjustment of the crop and the decrease in the total water potential, caused by the decrease in soil moisture.

Cruz (2006) has found significant decreases in leaf transpiration in maize genotypes subjected to water restriction. In those, relative transpiration decreased with soil water restriction and become practically zero, with 20% of available water in the soil (Bergonci and Pereira, 2002). Nable et al. (1999) have found decreases in E rates in sorghum and sugarcane plants as the fraction of available soil water decreased. Possibly, these decreases in cotton transpiration may be influenced by other factors, such as reduced leaf area (shedding) from the applied water deficit. Thereby, Bezerra et al. (2003) reported that osmotic stress reduces the availability of water to plants and may affect their gas exchange.

The variation in the mean values of the E rate among the cultivars was minimal throughout the evaluations, with mean value of 2.79, 3.18, 3.35, 3.82 and 3.99 m mol H_2O m^{-2} s^{-1} for the cultivars BRS 286 and BRS 336 (Table 5).

With these results, decrease could be observed in plant water flow, possibly because of the water deficit to which the cotton plant was subjected, which decreased the plant metabolism as the stomatal control of the E is a mechanism used by many species to restrict the loss of water and overcome periods of drought (Silva et al., 2003) and it probably seems to indicate cotton tolerance to avoid excessive loss of water. Much of the water absorbed by the cotton plant is used to cool it, to keep the leaf temperature at the optimum limit with dissipation as evaporation, thus favoring enzymatic activity (Echer, 2014).

Because of the decrease observed in gs and E, A was significantly compromised when the cotton plants were subjected to all water deficit periods, with mean values of 13.62, 15.93, 19.43, 9.90 and 11.93 μmol CO_2 m^{-2} s^{-1}, with decreases of 41.99, 33.06, 17.10, 60.80 and 25.53% in A at 29, 40, 54, 62 and 100 DAG, respectively, when compared to plants that were not subjected to stress (P1) (Table 6).

Therefore, there was a trend of greater sensitivity to water stress in all the different periods (cotton stages), as it reduced gs and E, as discussed previously, probably because of a decrease in the performance of the photosynthetic apparatus of the plants in relation to plants without water deficit (P1) (Table 6), as well as possibly because of the influence of the low water potential caused by the water deficit.

This confirms the results of Marenco and Lopes (2009), who stated that photosynthesis is directly affected by factors such as light intensity, temperature, CO_2 concentration, leaf nitrogen content and soil moisture.

A decline in the photosynthesis of cotton plants has also been verified by Meloni et al. (2003), Brito (2015) and Soares (2016) in those cultivated under irrigation with saline water. Probably, the soil water deficit caused a decrease in the photosynthesis of the cotton, as observed in this work.

Loka et al. (2011) stated that water deficit reduces the photosynthetic rate from a combination of stomatal and non-stomatal limitations. The stoma begins to close as a reaction to the decrease in leaf water potential, decreasing the rate of water loss, but also decreasing CO_2 entry and photosynthesis in the plant, which may have occurred here in treatments with water deficit.

The decrease in A may have been due to the closure of the stomata, which restricts the influx of CO_2 in the mesophyll cells. Stomata can respond quickly depending on the air or soil moisture (Turner et al., 1985).

The non-existence of oxygen, possibly because of stomatal closure, may induce a decrease in respiration, thus compromising the energy level, since active absorption needs energy resulting from the oxidative respiration and requires oxygen available in the soil (Souza et al., 1997).

Souza et al. (2000), studying the physiology and productivity of sesame in soils with water deficiency, have found decreases in photosynthesis after two days without irrigation, with a decrease of 88%. The same authors have found decreases in photosynthesis and respiration of 87 and 60%, respectively, with the application of water stress.

Although stomatal closure during the reduction of soil moisture coincides with the decrease in leaf water potential, several experiments have also shown decreases in gs, even though leaf water potential is kept constant (Davies et al., 1986; Gollan et al., 1986).

There is also evidence that dehydration, in addition to affecting photosynthesis from CO_2 flow restriction, has detrimental effects directly on the photosynthetic apparatus (Kaiser, 1987). Austin et al. (1982) and Johnson et al. (1987) have observed significant differences in photosynthesis among different wheat species.

According to Hsiao (1993), the difference in transpiration between plants results from differences in the efficiency of stomatal control, which has implications for the efficiency of water use, as well as stomatal control of transpiration; on the other hand, it imposes diffusion limitations for CO_2 that may lead to a decrease in the photosynthetic rate.

Researchers as Neves et al. (2009) and Silva et al. (2011) mentioned that the decrease in the photosynthesis rate is caused by partial stomatal closure associated with the osmotic effect and the ionic toxicity on the metabolism of the plants subjected to salinity conditions.

In this research, this decrease in the photosynthesis rate was probably caused by the water deficit to which the plants were subjected. James et al. (2002), states that both stomatal conductance and transpiration are reduced by the decrease in root water potential or by the transport of abscisic acid to the leaves.

Regarding the cultivar factor, photosynthesis was not affected in all periods of application of the water deficit (29, 40, 54, 62 and 100 DAG) with mean values of 21.23, 22.09, 22.28, 21.08 and 14.60 µmol CO_2 m^{-2} s^{-1} for the cultivars BRS 286 and BRS 336, respectively (Table 6), which are satisfactory values as cotton is a C_3 plant, with photosynthetic rates ranging between 10 and 20 µmol CO_2 m^{-2} s^{-1} (Taiz and Zeiger, 2013).

Possibly, the water stress imposed on cotton increased the leaf-to-air vapor pressure deficit (VPD$_{leaf-air}$), which can cause the water molecules to exit the stomatal cells into the external air, which is known as peristomatic evaporation (Maier-Maercker, 1983), promoting stomatal closure, especially in the treatments that were subjected to water deficit, minimizing the water exiting the cells.

Some researchers report in their work the negative effects of VPD$_{leaf-air}$ on gas exchange, which provides stomatal closure (Erismann et al., 2006; Costa and Marenco, 2007), thus reducing gs, E and A of plants, as observed in this work.

The mean values of *iWUE* were 7.59, 7.28, 6.95, 5.59 and 3.68 [(µmol CO_2 m^{-2} s^{-1}) / (mmol H_2O m^{-2} s^{-1})$^{-1}$] at 29, 40, 54, 62 and 100 DAG, respectively, which shows a decrease in *iWUE* as the water deficit was applied (Table 7).

As the *iWUE* is the result of the ratio of photosynthesis to transpiration, this fact is explained by the decrease in photosynthesis (CO_2 assimilation rate) in this study after 54 DAG (Table 6) from the decrease in water restriction. Lower absolute values can be observed for *iWUE* in the periods when the cotton plants underwent water restriction.

This decrease in *iWUE* observed in the treatments may be associated with a change in leaf transpiration and CO_2 assimilation rates (photosynthesis), possibly because of the low soil water availability, which induces the plant to the leaf osmotic adjustment, resulting in stomatal resistance and consequently reducing leaf transpiration and CO_2 assimilation rate, directly affecting *iWUE* as stated by Willadino and Camara (2004). Contradicting results have been found by Soares (2016) and Graciano et al. (2016), who have found a significant effect of the treatments studied on the iWUE. Larcher (2006) stated that the best ratio between photosynthesis and water consumption probably occurs when the stomata are partially closed, which can be demonstrated from the moment the water deficit starts when the two diffusion processes are readily decreased, which results in higher photosynthesis/transpiration ratio (A/E).

Therefore, the increase in iWUE of the cultivars evaluated in this work may have been favored by stomatal closure, observed from the results of gs, E and A. This result indicates that the cultivar that can keep a high A/E ratio under soil water deficit presents a higher tolerance to this condition.

In agreement with the results of gs, E and A, *Ci* presented the same trend observed for those variables in the treatments under water deficit, that is, the value of *Ci* decreased at 29 and 40 DAG, with mean value of 153.00 and 171.50 µmol CO_2 m^{-2} s^{-1}, respectively (Table 8).

Table 7. Mean values of instantaneous water-use efficiency at different evaluation ages of two upland cotton cultivars under different water deficit strategies in the phenological stages (Pombal county, Paraíba State, Brazil. 2015).

Factor (deficit periods)	Instantaneous water-use efficiency (*iWUE*)				
	29 DAG	40 DAG	54 DAG	62 DAG	100 DAG
P1	8.19[a]	7.36[a]	6.79[a]	5.97[a]	3.79[a]
P2	6.71[a]	7.59[a]	6.65[a]	5.74[a]	3.95[a]
P3	7.56[a]	7.58[a]	6.74[a]	5.81[a]	3.70[a]
P4	7.50[a]	6.60[a]	7.26[a]	5.23[a]	3.48[a]
P5	7.72[a]	7.01[a]	6.81[a]	4.48[a]	3.64[a]
P6	7.86[a]	7.42[a]	7.41[a]	6.32[a]	3.54[a]
General mean	7.59	7.28	6.95	5.59	3.68
(Cultivars)					
BRS 286	7.73[a]	7.45[a]	7.09[a]	5.63[a]	3.73[a]
BRS 336	7.45[a]	7.10[a]	6.80[a]	5.55[a]	3.63[a]
General mean	7.59	7.28	6.95	5.59	3.68

Same letters in the column indicate no significant difference among each factor level (Tukey, $p < 0.05$). DAG = days after germination.

Table 8. Mean values of internal CO_2 concentration at different evaluation ages of two upland cotton cultivars under different water deficit strategies in the phenological stages (Pombal county, Paraíba State, Brazil. 2015).

Factor (deficit periods)	Internal CO_2 concentration (*Ci*)				
	29 DAG	40 DAG	54 DAG	62 DAG	100 DAG
P1	199.25[a]	233.75[a]	189.20[a]	177.37[a]	202.00[a]
P2	153.00[b]	177.00[b]	177.64[a]	203.00[a]	200.75[a]
P3	215.87[a]	171.50[b]	196.67[a]	180.50[a]	205.12[a]
P4	190.62[a]	215.75[a]	153.80[a]	172.87[a]	197.25[a]
P5	220.62[a]	214.12[a]	188.18[a]	154.37[a]	183.00[a]
P6	191.87[a]	205.50[a]	183.89[a]	188.50[a]	185.37[a]
General mean	195.20	202.94	181.56	179.43	195.58
(Cultivars)					
BRS 286	191.45[a]	204.08[a]	177.83[a]	179.20[a]	193.95[a]
BRS 336	198.95[a]	201.79[a]	185.29[a]	179.66[a]	197.20[a]
General mean	195.20	202.94	181.56	179.43	195.58

Same letters in the column indicate no significant difference among each factor level (Tukey, $p < 0.05$). DAG = days after germination.

The deficit periods decreased *Ci* in 23.21% (P2), 26.63% (P3), 18.71% (P4), 12.96% (P5) and 8.23% (P6) at 29, 40, 54, 62 and 100 DAG, respectively, compared to the period without deficit (P1) (Table 8), probably because of the carbon flux for the synthesis of organic compounds, which were not being metabolized by the photosynthetic apparatus given the water stress condition to which the cotton plants were exposed at different water deficit periods.

The decreases recorded in Ci reflect the observed decreases in the rate of carbon dioxide assimilation, which is justified by the fact that, during the gas exchange process, the absorption of CO_2 converges in the loss of water and, conversely, the decrease in this water loss restricts the carbon dioxide assimilation and consequently converges to a lower internal CO_2 concentration (Shi Mazaki et al., 2007).

In addition, according to Jadoski et al. (2005), the Ci in the leaf mesophyll is reduced by the stomatal closure with a consequent decrease in the rate of carbon dioxide assimilation, which, in this work, was observed in all water deficit periods. On the other hand, Raschke (1979) and Dai et al. (1992) stated that the increase in the rate of CO_2 assimilation causes a decrease in evaluation ages, exerting a strong negative retroactive effect and, consequently, causing a decrease in the rate of CO_2

assimilation.

However, the above auhors reported that the decrease in Ci stimulates greater stomatal opening, thus allowing greater Ci for the substomatal cavity. It should be noted that, in this study, there was an increase in the rate of CO_2 assimilation in all deficit periods (29, 40, 54, 62 and 100 DAG) when compared to the period without deficit (P1), but only after irrigation return (Table 8). Larcher (2006) stated that values considered high for leaf Ci indicate that CO_2 is not being used for the synthesis of sugars by the photosynthetic process with the accumulation of this gas, which indicates that some non-stomatal factor is interfering in this process.

The increase in Ci can be attributed to the decrease in gs with the application of deficit periods, which is a common response in plants subjected to water stress. For Pereira et al. (2012), this type of behavior evidenced the occurrence of not only damage to the photosynthetic apparatus in the carboxylation stage but also an increase in the photorespiration process, since Ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBisCO) is the one that catalyzes the first step of this pathway.

Machado et al. (1999) stated that the increase in Ci can be related to the decrease in the activity of enzymes involved in the CO_2 fixation process. On the other hand Grassi and Magnani (2005) attributed this increase to non-stomatal factors, such as decrease in RuBisCO activity and concentration, photoinhibition, electron transfer rate and decreased photochemical efficiency of PSII, which may impair photosynthesis.

When evaluating the Ci of the cotton cultivars studied, mean values of 195.20, 202.94, 181.56, 179.43 and 195.58 µmol CO_2 mol^{-1} were observed at 29, 40, 54, 62 and 100 DAG for the cultivars BRS 286 and BRS 336, respectively (Table 8). These results are similar to those found by Ferraz (2012), who has studied the cultivars BRS Rubi, BRS Topázio and BRS Safira, under field conditions, with mean values ranging from 182.9 to 223.7 µmol CO_2 mol^{-1}, however these values are higher than those found by Soares (2016) for these same cultivars, who has obtained mean values ranging from 154.69 to 172.39 µmol CO_2 mol^{-1}.

On the other hand, Freire et al. (2014), studying yellow passionfruit plants under saline stress, have recorded Ci of 259.70 and 229.47 µmol CO_2 mol^{-1} in plants that did not undergo saline stress, this serves as evidence for the negative effects of stress on the plant carbon metabolism. For Larcher (2006), high concentrations of Ci in the substomatal cavity of leaves mean that CO_2 is not being used by photosynthesis, which indicates that some non-stomatal factor is interfering in this metabolic process.

The iCE is a way of studying the non-stomatal factors that interfere with the photosynthetic rate, since this parameter has a close relation with Ci and with the rate of CO_2 assimilation (Konrad et al. 2005; Machado et al. 2010). At 29 and 62 DAG, the effect of the periods of

water deficit can be observed on iCE with mean values of 0.12 and 0.06 ((µmol CO_2 m^{-2} s^{-1}) / (µmol CO_2 mol^{-1})$^{-1}$) and decreases in iCE of 33.33% and 57.14%, compared to plants that did not undergo water deficit (P1) (Table 9).

Probably, the decrease in iCE may be related to the higher Ci in plants, also under water deficit in the boll formation stage, when there is a high water demand for fruit growth, which causes the plant to adapt and close the stomata more effectively. This decrease is probably a reflection of the low CO_2 assimilation in relation to the CO_2 found in the substomatal cavity in these plants, because, if Ci increases and there is a decrease in CO_2 consumption in chloroplasts from the decreased photosynthetic activity, the A/Ci ratio will also decrease (Suassuna, 2013).

A decrease in iCE can be observed at 40, 54 and 100 DAG in the periods of water deficit with mean values of 0.11, 0.12 and 0.07 [(µmol CO_2 m^{-2} s^{-1}) / (µmol CO_2 mol^{-1})$^{-1}$], as well as in the treatments that again had irrigation from the possible recovery and not in the treatments of flower bud (P3), flower (P5) and open boll (P6), as the deficit was not enough to cause differences in this variable. In the treatments that had a significant effect, the lowest mean values were observed in the treatments with water deficit (Table 9). Even so, iCE has a close relation with the intracellular concentration of CO_2 and the rate of carbon dioxide assimilation (Machado et al., 2005).

For the cultivar factor, in the periods of water deficit (29, 40, 54, 62 and 100 DAG), the mean values were 0.11, 0.11, 0.12, 0.12 and 0.07 ((µmol CO_2 m^{-2} s^{-1}) / (µmol CO_2 mol^{-1})$^{-1}$) for the cultivars BRS 286 and BRS 336, respectively (Table 9).

Opposite results have been found by Soares (2016), who has studied the tolerance of colored cotton genotypes to saline stress in the different phenological stages, in which there was a significant decrease in iCE in all cultivars studied with the restriction of available soil water. Considering that the cotton plants were subjected to different conditions of water deficit according to their phenological stages, when gas exchange were also measured, it is assumed that the deficit caused by the water restriction reached the water status of the plant at the stomatal level.

Nevertheless, according to Marenco and Lopes (2009), in situations of moderate or severe water deficit, stomatal resistance may occur from the increase in the diffusion of the acid towards the guard cells, whereas the stomata tend to remain open in mild stress. Padilha et al. (2016) stated that the abscisic acid induces stomatal closure, as long as its synthesis is stimulated by water scarcity. In these circumstances, stomatal closure is related to the decrease in leaf water potential (Pereira, 2012).

Therefore, it is believed that the cotton plants, in the different evaluation periods, reached cellular turgescence with potential to cause stomatal changes. Thus, when the gas exchange in plants under water deficit exhibits

Table 9. Mean values of instantaneous carboxylation efficiency at different evaluation ages of two upland cotton cultivars under different water deficit strategies in the phenological stages (Pombal county, Paraíba State, Brazil. 2015).

Factor (deficit periods)	Instantaneous carboxylation efficiency (*iCE*)				
	29 DAG	**40 DAG**	**54 DAG**	**62 DAG**	**100 DAG**
P1	0.12[a]	0.10[a]	0.12[a]	0.14[a]	0.07[a]
P2	0.08b	0.12[a]	0.13[a]	0.12[a]	0.07[a]
P3	0.10[a]b	0.09[a]	0.11[a]	0.13[a]	0.07[a]
P4	0.11[a]b	0.11[a]	0.12[a]	0.12[a]	0.07[a]
P5	0.10[a]b	0.10[a]	0.13[a]	0.06b	0.08[a]
P6	0.12[a]	0.11[a]	0.12[a]	0.13[a]	0.06[a]
General mean	0.11	0.11	0.12	0.12	0.07
(Cultivars)					
BRS 286	0.11[a]	0.11[a]	0.12[a]	0.12[a]	0.07[a]
BRS 336	0.10[a]	0.10[a]	0.12[a]	0.11[a]	0.07[a]
General mean	0.11	0.11	0.12	0.12	0.07

Same letters in the column indicate no significant difference among each factor level (Tukey, $p < 0.05$). DAG = days after germination.

different behavior than that without water restriction, the effects of soil water deficit probably interfere with the photosynthetic processes of the plants.

The results found for Ci followed the same trend of gs and E (except at 54 DAG) as the stomatal movement is the mechanism that regulates the gas exchange and increases in gs, which means a greater influx of CO_2 for the leaf mesophyll, resulting in higher rates of carbon dioxide assimilation (Shi Mazaki et al., 2007). The treatments (deficit periods) that resulted in an increase in gs, Ci and E, consequently had greater photosynthesis, which denotes close connection, since gs allows a greater entry of CO_2, directly influencing the photosynthetic performance (Pereira, 2012).

The decreases in the variables of gas exchange studied in this work probably occurred because of the decrease of energy in the root water potential and/or the transport of the abscisic acid to the leaves, which reflect an increase in stomatal resistance and a decrease in carbon concentration in the substomatal cavity. This is explained by the direct relation between gas exchange (implied CO_2 absorption) and water loss, in which stomatal closure results in decreased E and, consequently, lower Ci (Shi Mazaki et al., 2007), which probably induces a decrease in A, iWUE and iCE.

These decreases may also be associated with a decrease in amylaceous reserves in cotton leaves under conditions of water deficit that can be explained considering that soil water deficit may lead to decreases in assimilate synthesis and consequently starch reserves are rapidly used for plant metabolism, which is why the contents of soluble sugars are stable when cotton plants are induced to water deficit (Souza and Silva, 1983; Souza et al., 2000), thus corroborating Souza et al. (2000), who stated that the physiological behavior of sesame was influenced by soil water deficit.

Depending on the duration of the soil water deficit, the cotton plant underwent physiological changes in all the periods subjected to the deficit and although the photosynthetic activity is changed at fourteen days of soil water deficit, the plants can recover after its suspension and the return of irrigation, depending on the duration of irrigation. The decrease in the photosynthetic activity of the cotton plant that occurred when subjected to water deficit may be due to its stomatal closure efficiency to reduce cotton gas exchange and transpiration.

Conclusion

Water deficits reduced the gas exchange of the upland cotton plants, mainly stomatal conductance, transpiration and photosynthesis; the cotton cultivars BRS 286 and BRS 336 presented similar behavior in the different water deficits applied on different phenological stages; cotton was less tolerant to water deficits in the boll formation stage; and, cotton was more tolerant to water deficit in the initial growth and flower bud stages.

CONFLICT OF INTERESTS

The authors have not declared any conflict of interests.

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