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BIOLOGY

Daytime gas exchange in soybean plants submitted to waterlogging and shading

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ABSTRACT: Aerobic respiration declines in the root tissue of soybean plants exposed to waterlogged soil with a low oxygen content, causing metabolic disorders that negatively affect gas exchange and photosynthetic activity, hampering growth and production. As such, this study to investigated daytime gas exchange, relative chlorophyll content, specific leaf area (SLA) and photosynthetic activity curves in response to photosynthetic photon flux density (PPFD) in soybean plants grown under different conditions: no stress (control), shading, waterlogged soil, and waterlogged soil + shading. Soybean plants exposed to either waterlogging or shading and both conditions simultaneously exhibited reduced photosynthesis linked to lower stomatal opening. Plants submitted to shading showed an increase in SLA, quantum yield and photosynthetic rates, while those grown in waterlogged soil, in full sun, exhibited chlorotic leaves and low apparent quantum yield, resulting in low photosynthetic rates under shading and high light levels. Thus, waterlogging and shading in isolation or combined, compromise daytime gas exchange and alter photosynthetic activity in plants.
Key words: environmental stress, *Glycine max* L., photosynthetic activity.

Trocas gasosas ao longo do dia de plantas de soja submetidas ao encharcamento do solo e restrição luminosa

RESUMO: Os tecidos radiculares de plantas de soja em solo encharcado, com baixo teor de oxigênio, apresentam reduzida atividade da respiração aeróbica, causando desordens metabólicas que afetam negativamente as trocas gasosas e atividade fotossintética, prejudicando o crescimento e produção. Assim, o estudo teve como objetivo investigar as trocas gasosas ao longo do dia, teor relativo de clorofila, área foliar específica e curvas de atividade fotossintética em resposta à densidade de fluxo de fótons fotossinteticamente ativos de plantas de soja desenvolvendo em condições ambientais distintas: sem estresse, com restrição luminosa, em solo encharcado, e em solo encharcado + restrição luminosa. As plantas de soja expostas ao encharcamento do solo e a restrição luminosa de forma isolada ou em conjunto apresentaram redução da fotossíntese associada à menor abertura estomática. Plantas submetidas a restrição luminosa apresentaram folhas com incremento na área foliar específica, maior eficiência quântica aparente e incremento nas taxas fotossintéticas em ambiente com baixa luminosidade. Plantas em solo encharcado, a pleno sol, apresentaram folhas cloróticas e baixa eficiência quântica aparente e consequentemente apresentaram baixas taxas fotossintéticas sob luminosidade baixa e luminosidade elevada. Desta forma, o encharcamento do solo e restrição luminosa de forma isolada ou conjunta prejudicam as trocas gasosas ao longo do dia e causam alterações na atividade fotossintética das plantas.
Palavras-chave: estresse ambiental, *Glycine max* L., atividade fotossintética.

INTRODUCTION

Soybean (*Glycine max* L.) is grown in different regions worldwide, some of which are subject to unfavorable environmental conditions. Excess rainfall and cloud cover can compromise soybeans crops by causing waterlogging and restricting sunlight. Soybean plants grown in waterlogged soil are subject to development problems. Waterlogged soil is characterized by excess water that occupies pore space, resulting in low oxygen content. For roots, low oxygen concentration, known as hypoxia, compromises oxygen-dependent aerobic respiration, causing metabolic disorders (BAILEY-SERRES et al., 2012).

High anerobic metabolism in hypoxic root tissue can lead to chlorosis, partly because greater anerobic activity increases the concentration of substances that degrade proteins, making leaves chlorotic. Another noteworthy point is that plants with hypoxic roots exhibit a higher leaf ethylene content (IRFAN et al., 2010), thereby increasing chlorophyllase and oxidase activity, enzymes that degrade chlorophyll and cause chlorosis (DALMOLIN et al. 2012). Hypoxic roots are also less

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able to absorb water, which lowers water potential and increases abscisic acid (ABA) production in the roots, thus raising leaf levels of the hormone and causing stomatal closure, modifying gas exchange (ASHRAF, 2012).

Soybean plants grown in low-light environments also exhibit poor development (WU et al., 2017a), since the reduced incident solar radiation on leaves compromises stomatal opening and alters leaf gas exchange processes (SU et al., 2014). Low light levels also reduce the synthesis of metabolic energy due to the decline in photosynthetic apparatus activity, with poor availability of metabolic energy resulting in less organic compound synthesis in the Calvin-Benson cycle. Thus, soybean plants exposed to insufficient light exhibit reduced net CO_2 assimilation (WU et al., 2016).

It should be noted that in order to mitigate the damage caused by low light, plants may undergo changes to increase their light capture and use efficiency, such as wider leaves, a higher chlorophyll content and greater investment in the antenna complex of the photosynthetic apparatus (SU et al., 2014; WU et al., 2016).

In this context, the present study investigated daytime gas exchange, relative chlorophyll content, specific leaf area and photosynthetic activity as a function of photosynthetic photon flux density (PPFD).

MATERIALS AND METHODS

The experiment was conducted at the Horticulture and Protected Cultivation Center in Marechal Cândido Rondon, Paraná state (PR), from December 2018 to April 2019.

The soybean plants were exposed to four different environmental conditions: normal irrigation in full sunlight (no stress); normal irrigation and shading (no waterlogging + shading); waterlogged soil in full sunlight (waterlogging + no shading); and waterlogged and shading (waterlogging + shading). A randomized block design with five repetitions and two plants per repetition was used.

The Bayer 2606® IPRO soybean cultivar was used, grown in 8.7 dm³ pots containing soil from horizon A of a eutrophic red latosol, with two plants per pot (SANTOS et al., 2018). In order to restrict light levels, twelve 1.5 m-high wooden frames (1.5 m x 1 m) were constructed and covered with 80% shade cloth. In the waterlogging treatments, the soil was maintained above field capacity, with the pots constantly submerged in 0.15 m of water within wooden structures (0.5 m x 0.5 m and 0.2 m high) covered in black canvas sheeting. The treatments were applied simultaneously, for 15 days, from the onset of the full flowering stage (R_2).

Gas exchange was measured 15 days after treatment onset at 6, 8 and 10 a.m. and 12, 2, 4 and 6 p.m. (BRT time zone, UTC offset of -03:00), using an Li-6400XT infrared gas analyzer (IRGA) to determine net CO_2 assimilation (A) (µmol CO_2 m^{-2} s^{-1}); transpiration (E) (µmol H_2O m^{-2} s^{-1}), stomatal conductance (g_s) (mol m^{-2} s^{-1}) and internal CO_2 concentration (µmol CO_2 mol^{-1}). Weather conditions in the full sun and shaded environments were also determined, namely PPFD (µmol m^{-2} s^{-1}) (DFFFA) temperature (ºC), relative humidity (%) and vapor pressure deficit (kPa) (ZHANG et al., 2001).

The SPAD index and SLA were also measured on the same date. Relative chlorophyll content (SPAD index) was determined using a chlorophyll meter (SPAD 502 Plus; Konica Minolta). For SLA, four leaves were collected, and their areas measured (cm²). The leaves were then dried in an oven to determine dry weight (g), which was divided by leaf area to establish SLA (cm^2 g^{-1}) (GOBBI et al., 2011).

Net CO_2 assimilation as a function of PPFD was measured 15 days after treatment onset using an Li-6400XT infrared gas analyzer (IRGA). The readings were taken between 8 and 11 a.m. on fully developed photosynthetically active leaves with no apparent injuries, located on the middle third of the plants. The following PPFD values were used: 0, 25, 50, 75, 100, 250, 500, 1000, 1500, 2000 and 2500 µmol m^{-2} s^{-1}.

Data on CO_2 assimilation responses to PPFD of 0, 25, 50, 75, 100 and 250 µmol m^{-2} s^{-1} of photons were used to determine apparent quantum yield (Φ [µmol photons / µmol CO_2]), adjusting the equation ($A = a + \Phi PPFD$), where Φ are the adjustment coefficients, obtained by inverting the angular coefficient. The value of the light compensation point [Γ (µmol m^{-2} s^{-1})] was calculated at the intersection of the straight line with the x axis. The response curve of A to PPFD was adjusted using the rectangular hyperbola function ($A = Amax$PPFD/ "a" + PPFD), where $Amax$ is the maximum photosynthetic rate and "a" the adjustment coefficient of the equation (MACHADO et al., 2005).

The data were submitted to analysis of variance (ANOVA) and compared by Tukey's test, both at 5% probability, using SISVAR 5.1 software (FERREIRA, 2014).

RESULTS

Weather conditions during daytime gas exchange readings

Average PPFD during the gas exchange readings was around 75% lower in the shaded

environments when compared to full sun conditions (Figure 1A). Average temperature, relative humidity and vapor pressure deficit (VPD) were similar between the full sun and low-light environments at the different assessment times. It should be noted that the shade cloth contains holes that allow air from the (outdoor) sunlit environment to travel through the shaded structures, which likely explains the similar average values recorded between environments (Figure 1).

Daytime gas exchange, relative chlorophyll content and specific leaf area

The 15 days of exposure to waterlogged soil and/or shading during the full flowering stage (R_2) caused changes in net photosynthesis (*A*), transpiration (*E*), stomatal conductance (*gs*) and internal CO_2 concentration (*Ci*) (Figure 2).

Figure 2A shows the data on *A* at different times of day. The results indicated that, when compared to soybean plants grown under full sun and no waterlogging, those without waterlogging in a shaded environment exhibited a decline in *A* ranging from 48% at 6 a.m. to 18% at 2 p.m., which then increased to 55% at 6 p.m.

Plants in waterlogged soil under full sunlight also showed an approximate 41 to 50% reduction in *A* across the assessment times in relation to stress-free plants. Additionally, waterlogged soil with shading decreased *A* by about 55 (6 p.m.) to 18% (2 p.m.) in relation to the stress-free treatment (control).

Under normal irrigation with low light, *E* declined by 22 and 45% at 10 a.m. and 6 p.m., respectively, when compared to plants without stress, while those submitted to waterlogging and shading produced 19 and 34% lower *E* readings at 10 a.m. and 6 p.m., respectively, in relation to their stress-free counterparts. For plants in waterlogged soil with no sunlight restrictions versus controls, there was a 27 (10 a.m.) to 50% (6 p.m.) reduction in *E* (Figure 2B).

Regarding *gs*, soybean plants under normal irrigation with shading exhibited decreases of 26, 28 and 46% at 8 and 10 a.m. and 6 p.m., respectively, when compared to the treatment without stress. Declines were also observed for the waterlogging + shading treatment of 26, 23 and 40% at 8 and 10 a.m. and 6 p.m., respectively, in relation to controls, with

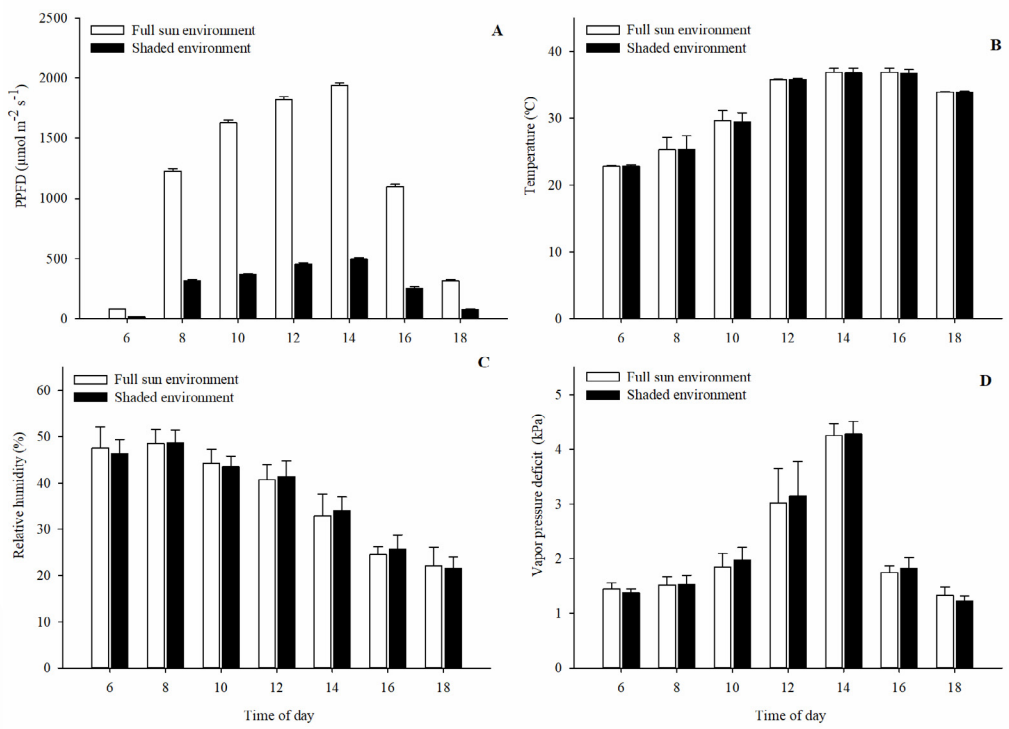

Figure 1 - Weather conditions in the shaded environment and under full sun, average photosynthetic photon flux density (PPFD) (DFFFA) (A) and average temperature (B), relative humidity (C) and vapor pressure deficit (D) at the gas exchange assessment times. The bars in the columns represent standard deviation.

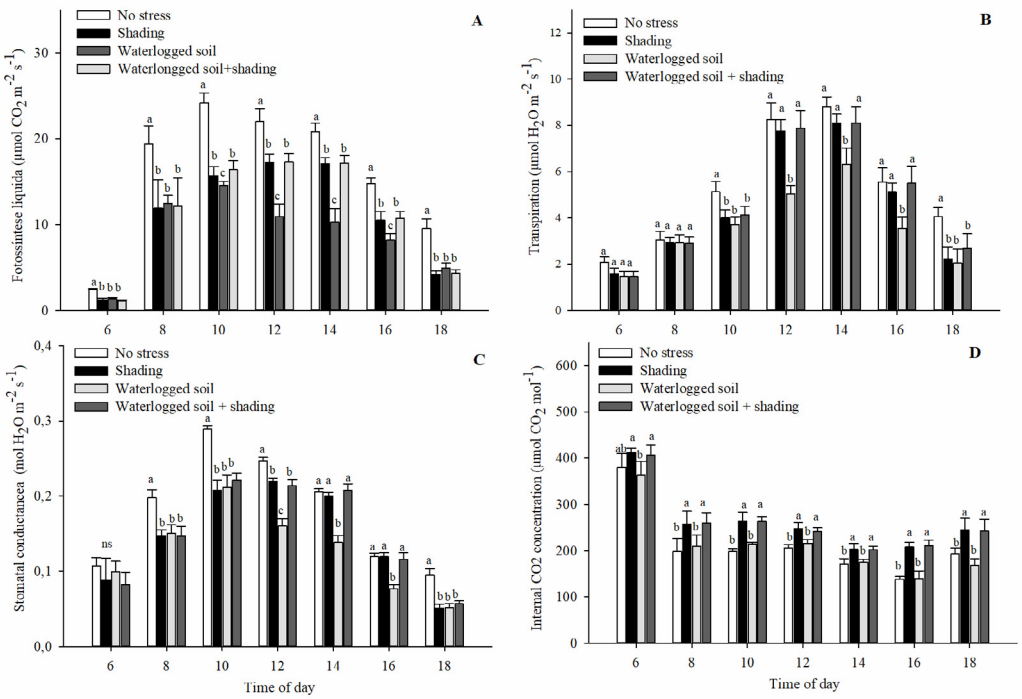

Figure 2 - Net photosynthesis (A), transpiration (B), stomatal conductance (C) and internal CO_2 concentration (D) measured on the leaves of Bayer 2606® IPRO soybean plants. The data were obtained 15 days after full flowering onset (R_2), when the treatments with the presence and absence of shading and waterlogging were applied. Means followed by the same lowercase letters in the column do not differ according to Tukey's test at 5% probability. ns not significant. The bars in the columns represent standard deviation.

reductions of 24 (8 a.m.) to 45% (6 p.m.) for plants in waterlogged soil under full sunlight (Figure 2C).

Figure 2D presents the *Ci* data for the different assessment times. The results demonstrate that plants submitted to normal irrigation with shading obtained *Ci* values around 30, 33, 20, 18, 50 and 27% higher than those of controls at 8 and 10 a.m. and 12, 2, 4 and 6 p.m., respectively, whereas *Ci* increased by approximately 31, 33, 1, 18, 52 and 25% at the same assessment times in plants grown in waterlogged soil with shading.

In plants with no waterlogging and low light levels, *Ci* was about 23% (8 a.m.) higher when compared to those grown in waterlogged soil under full sunlight, declining to 16% (2 p.m.) and then increasing at the 6 p.m. reading (46%). Similarly, plants in waterlogged soil under shade exhibited 24% higher *Ci* at 8 a.m. than those under the same soil treatment with full sun, reaching 15% at 12 p.m. and rising to 51% at 4p.m.

Figure 3A presents the data on relative chlorophyll content (SPAD index). Plants submitted to waterlogging and full sun showed a 13, 12 and 12% decline in the SPAD index in relation to the control, normal irrigation + shade and waterlogging + shade treatments, respectively (Figure 3A).

Figure 3B depicts the leaf surface area (LSA) data. The findings indicate that plants under normal irrigation with shade and those exposed to waterlogged soil and shade obtained LSA values around 74 and 77% higher, respectively, than those of stress-free controls, and 77 and 81% greater when compared with the waterlogging + full sun treatment.

Response to photosynthetic photon flux density

Exposure to waterlogged soil and shading for 15 days altered pant responses to PPFD (Figure 4). Maximum CO_2 assimilation (peak net photosynthesis) occurred at 2500 µmol photons m^{-2} s^{-1}, reaching 25.45, 27.49, 27.75 and 17.12 µmol CO_2 m^{-2} s^{-1} in plants grown under normal irrigation with full sun (no stress), normal irrigation with shading, waterlogged and shading, and waterlogged with full sun (Figure 4A).

Plants submitted to shading, both under normal irrigation and grown in waterlogged soil,

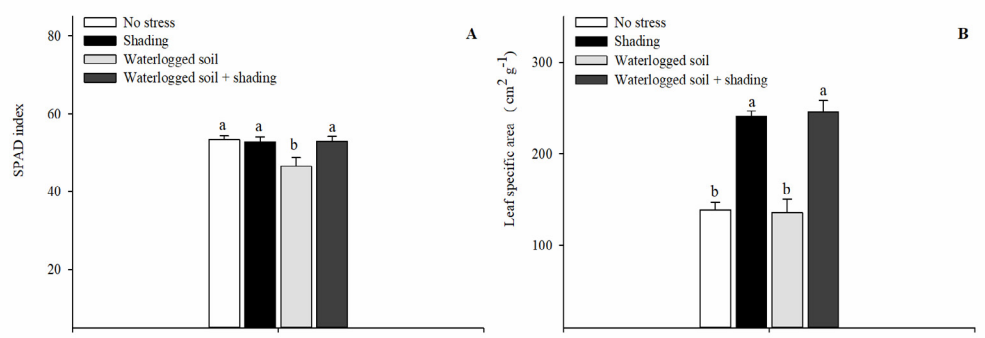

Figure 3 - Relative chlorophyll content (SPAD index) (A) and specific leaf area (B) of Bayer 2606® IPRO soybean plants. The data were obtained 15 days after full flowering onset (R_2), when the treatments with the presence and absence of shading and waterlogging were applied. Means followed by the same lowercase letters in the column do not differ according to Tukey's test at 5% probability. ^{ns} not significant. The bars in the columns represent standard deviation.

exhibited similar apparent quantum yield (Φ) (Figure 4B), requiring 18.28 and 18.25 µmol photons m^{-2} s^{-1} to fix 1 µmol CO_2, respectively. Additionally, stress-free plants and those in waterlogged soil under full sun needed 20.49 and 30.03 µmol photons m^{-2} s^{-1} to fix 1 µmol CO_2, respectively.

DISCUSSION

Soybean plants submitted to waterlogged soil and shading for 15 days from the onset of full flowering showed changes in daytime gas exchange (Figure 2) and photosynthetic activity (Figure 4). For plants under waterlogging and full sun, gas exchange alterations were associated with low soil oxygen availability. Hypoxia in roots can cause root suberization or lignification, lowering aquaporin activity and, consequently, reducing water absorption capacity (KARLOVA et al., 2021). As such, hypoxic roots exhibit less hydraulic conductivity, which decreases plant water potential. In plants, low water potential increases abscisic acid (ABA) production in the roots, raising leaf concentration of the hormone and causing stomatal closure (MENG & FRICKE, 2017).

Hypoxic roots can; therefore, cause metabolic and morphological changes that alter plant-water relations and reduce stomatal opening. This results in low *gs* and contributes to reducing *E* in plants grown in waterlogged soil under full sun when compared to their stress-free counterparts (Figure 2). For plants under hypoxic conditions, the decline in stomatal opening may be a survival strategy to minimize water loss through transpiration due to reduced water uptake (DALMOLIN et al., 2012).

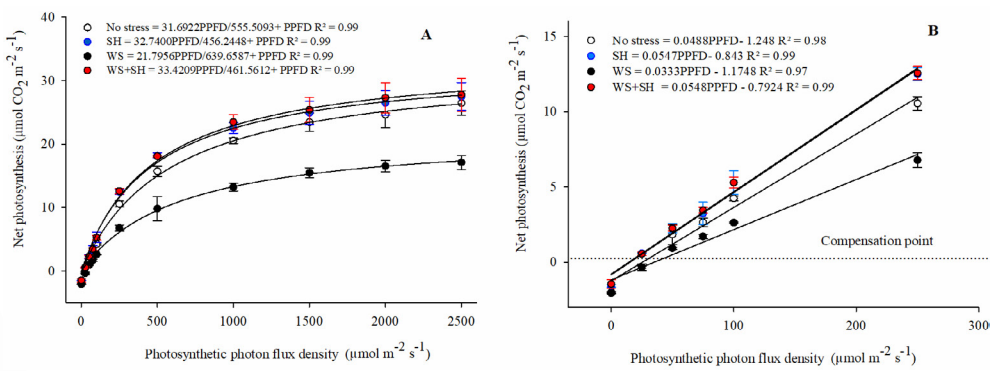

Figure 4 - Net photosynthesis (A) in soybean leaves in response to photosynthetic photon flux density (PPFD) of 0 to 2500 µmol photons m^{-2} s^{-1}. Apparent quantum yield (B) in response to photosynthetic photon flux density (PPFD) of 0 to 250 µmol photons m^{-2} s^{-1}. The data were obtained in Bayer 2606® IPRO soybean leaves 15 days after full flowering onset (R_2), when the treatments with the presence and absence of waterlogged soil (WS) and shading (SH) were applied. The bars represent the standard deviation.

A smaller stomatal opening in plants with hypoxic roots also compromises CO_2 diffusion through the stomata into the leaf, which can negatively affect CO_2 by plants grown in waterlogged soil (ZHANG et al., 2019). This is confirmed by the concomitant decline in *A* and *gs* in all the readings (Figure 2). It is also important to underscore that despite the reduced CO_2 assimilation rate, plants exposed to waterlogging under full sun obtained similar *Ci* values to their stress-free counterparts (Figure 2D). This reinforces the idea that a small stomatal opening hampered CO_2 supply in leaves.

Low leaf CO_2 content in soybean plants exposed to waterlogged soil under full sun (Figure 2D) increases the O_2:CO_2 ratio and, consequently, the oxygenase activity of the RUBISCO enzyme due to low CO_2 availability (ZHU et al., 2010). The rise in RUBISCO oxygenase activity increases photorespiration and reduces net photosynthesis by releasing the previously fixed CO_2 from the Calvin-Benson cycle at the end of the reactions (TAIZ et al., 2017). As such, the higher photorespiration rate contributed to reducing net photosynthesis throughout the day in plants grown in waterlogged soil with full sun (Figure 2A).

Another noteworthy point is that exposure to waterlogged soil alters the expression of genes associated with the circadian cycles. The circadian clock regulates vital activities during the day/night and there is evidence that drought stressed soybean plants alter gene expression to restore the balance between energy metabolism and photosynthesis (SYED et al., 2015). MEDINA-CHÁVEZ et al. (2023) found that, at the beginning of the second day of exposure to waterlogged soil, *Brachypo diumdistachyon* showed negative control of photosynthetic processes, possibly as a defensive strategy against oxidative stress caused by waterlogging under full sun. This helps explain the decline in net photosynthesis in plants grown in waterlogged soil with no light restrictions (Figure 2A).

Soybean plants exposed to waterlogging under full sun also displayed a lower relative chlorophyll content (Figure 3A), with their chlorotic leaves also corroborating the decline in CO_2 assimilation (SOUZA et al., 2013).

The reduced SPAD index in waterlogged plants under full sun (Figure 3A) helps explain the considerable decrease in *A* at the different assessment times (Figure 2A). This is consistent with the lower apparent quantum yield between treatments in plants under full sunlight in waterlogged soil (Figure 4B), since the decline in relative chlorophyll content (Figure 3B) likely caused a considerable decrease in photon use in CO_2 assimilation.

The lower SPAD index in the waterlogged + full sun treatment is associated with greater oxidative stress in the photosynthetic apparatus of these plants. Exposure to full sunlight in waterlogged plants (Figure 1A) causes significant NADPH and metabolic energy (ATP) production. However, low internal CO_2 concentration (Figure 2D) reduces activity in the Calvin-Benson cycle, thus lowering NADPH and ATP consumption and the availability of NADP and ADP carriers, which move electrons and energy through the electron transport chain on the thylakoid membrane (FOYER & NOCTOR, 2009).

The low availability of NADP and ADP carriers overloads photosystem II by reducing the transfer of the light energy received. The excess electrons in the photosystems are dissipated in carotenoids or captured by oxygen, forming reactive oxygen species (BARBOSA et al., 2014). As such, for plants in waterlogged soil, this oxidative stress contributes to lowering chlorophyll content under full sun when compared to those grown under shade. However, the low-light plants did not exhibit the necessary conditions for developing oxidative stress (Figure 1A) and showed a high internal CO_2 concentration (Figure 2D).

Thus, shading caused acclimation that prevented chlorophyll content from declining in the waterlogged + shading treatment, contributing to the similar gas exchange and photosynthesis behavior observed when compared to plants under normal irrigation with shade (Figures 2 and 4).

For plants in the low-light environment, the reductions in *A*, *E* and *gs* (Figure 2) are linked to the lower incidence of solar radiation. The processes involved in gas exchange and photosynthesis are highly sensitive to light levels (KHALID et al., 2019). Thus, it is important to underscore that the average PPFD of the plant canopy was approximately 75% lower in the shaded environment at the different assessment times when compared with the canopy under full sun (Figure 1A).

Although, data from the leaf gas exchange readings indicated a substantial decline in net photosynthesis (Figure 2A), it should be noted that the values are not proportional to the reduction in incident solar radiation (Figure 1A). This is associated with the fact that the shaded plants showed greater apparent quantum yield than their stress-free counterparts and those in waterlogged soil under full sun (Figure 4B).

For soybean plants submitted to shading, greater photon use efficiency may be the result of the increase in total chlorophyll content and decline in

chlorophyll a:b ratio, indicating greater investment in the antenna complex. These changes contribute to better use of solar radiation and, consequently, smaller losses in net photosynthesis (SU et al., 2014; WU et al., 2016).

The gas exchange data also indicates that the decline in net photosynthesis at different times in the shaded plants, whether waterlogged or not (Figure 2A), is not related to lower stomatal opening. Despite the smaller stomatal opening observed at 8 and 10 a.m. and 12 and 6 p.m. (Figure 2C), internal CO_2 concentration was higher than that of plants without stress, regardless of the time (Figure 2D). This finding demonstrated that reduced stomatal opening did not hamper leaf CO_2 diffusion and therefore did not limit its availability for photosynthesis, likely due to the increase in SLA in the shaded plants (Figure 3B). The rise in SLA is associated with the fact that plants grown under low light levels have wider and thinner leaves than those under full sun (TAIZ et al., 2017). This reduced thickness is the result of thinner palisade parenchyma cells and/or a smaller number of layers. Thus, the thinner mesophyll makes it possible to maintain CO_2 supply to the assimilation site despite smaller stomatal opening, causing a greater decline in net photosynthesis in shaded plants (WU et al., 2017b).

CONCLUSION

Plants grown in waterlogged soil with shading for 15 days from the onset of full flowering (R_2) show gas exchange modifications and reduced photosynthesis at different times of day.

Additionally, shaded plants acclimatize to the growing conditions, enabling them to use incident radiation more efficiently.

Conversely, plants in waterlogged soil under full sun exhibit chlorosis and greater photosynthetic losses associated with low light use efficiency and stomatal opening at the hottest times of day.

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DECLARATION OF CONFLICT OF INTEREST

The authors declare that there are no conflicts of interest.

AUTHORS' CONTRIBUTIONS

All the authors contributed equally to the study and writing of the manuscript.

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