AGRONOMY (AGRONOMIA)

Revista Brasileira de Ciências Agrárias
ISSN (on line) 1981-0997
v.17, n.2, e696, 2022
Recife, PE, UFRPE. www.agraria.pro.br
DOI: 10.5039/agraria.v17i2a696 - Protocol 696
Subm. 06/05/2021 • App. 04/05/2022 • Pub. 11/06/2022

Gas exchanges and soybean plant production in response to waterlogged soil and light restriction

Roberto Cecatto Júnior[1*], Vandeir Francisco Guimarães[1], Lucas Guilherme Bulegon[1], Anderson Daniel Suss[1], Tauane Santos Brito[1], Olivia Diulen Costa Brito[1]

[1] Universidade Estadual do Oeste do Paraná, Marechal Cândido Rondon, PR, Brasil. E-mail: junior_cecatto@yahoo.com; vandeirfg@yahoo.com.br; lucas_bulegon@yahoo.com.br; andersuss@hotmail.com; tauane-brito@hotmail.com; odc.brito@gmail.com

ABSTRACT: Soybean plants grown in waterlogged soil and a low-light environment show losses in growth and production. Thus, the objective of this study was to investigate the chlorophyll content, foliar nutrient content, gas exchanges, dry matter accumulation and the production of soybean plants submitted to waterlogged soil and light restriction. The first factor was the presence and absence of waterlogged soil; the second was the presence and absence of light restriction. For the treatments with waterlogged soil, it was kept above the field capacity. For the imposition of the light restriction, a shading screen, with the capacity to retain 80% of the incident light, was used. The treatments impositions occurred simultaneously, starting at full bloom (R_2), lasting for 30 days until the beginning seed ($R_{5.2}$). Plants submitted to waterlogged soil and light restriction showed a reduction on the liquid photosynthetic rate, transpiration, and stomatal conductance. Plants conducted in waterlogged soil in full sun showed chlorotic leaves with reduced levels of foliar nutrients and dry matter accumulation. Thus, the waterlogged soil and/or light restriction, for a 30-day period, from R_2, negatively affect the photosynthesis, the dry matter accumulation and causes less soybean production.

Key words: environmental stress; *Glycine max* L.; photosynthetically active photon flux density

Trocas gasosas e produção de plantas de soja em resposta ao encharcamento do solo e restrição luminosa

RESUMO: Plantas de soja cultivadas em solo encharcado e ambiente com baixa luminosidade apresentam menor crescimento e produção. Assim, o estudo teve como objetivo investigar o teor de clorofila, teor de nutrientes foliares, trocas gasosas, acúmulo de matéria seca e produção de plantas de soja em solo encharcado e restrição de luminosa. O primeiro fator foi presença e ausência de solo encharcado; o segundo foi presença e ausência de restrição luminosa. Para os tratamentos com solo encharcado, manteve-se acima da capacidade de campo. Para a imposição da restrição luminosa, foi utilizada uma tela de sombreamento, com capacidade de reter 80% da luz incidente. A imposição dos tratamentos ocorreu simultaneamente, iniciando no pleno florescimento (R_2), com duração de 30 dias até o início do enchimento de grãos ($R_{5.2}$). Plantas em solo encharcado e restrição luminosa apresentam redução da taxa fotossintética líquida, transpiração e condutância estomática. Plantas em solo encharcado a pleno sol apresentam folhas cloróticas com menores teores de nutrientes foliares e redução do acúmulo de matéria seca. Assim, o encharcamento do solo e/ou restrição luminosa, por um período de 30 dias, a partir de R_2, interferem negativamente na fotossíntese, acúmulo de matéria seca e causa menor produção de soja.

Palavras-chave: estresse ambiental; *Glycine max* L.; densidade de fluxo de fótons fotossinteticamente ativos

* Roberto Cecatto Júnior - E-mail: junior_cecatto@yahoo.com (Corresponding author)
Associate Editor: Mário de Andrade Lira Júnior

Introduction

Soybean (*Glycine max* L.) is a crop of great importance for global agribusiness. For this reason, researchers seek to study the consequences of soybean exposure to unfavorable environmental conditions, to increase the knowledge about metabolic responses and to comprehend the negative effects caused by such conditions.

The soybean cropping occurs in most regions of the world, and there may be production areas subjected to stress conditions caused by environmental factors adverse to the crop. In this way, excessive precipitation and cloudiness can occur, promoting unfavorable conditions, such as waterlogged soil (Beutler et al., 2014) and low incident light (Yang et al., 2017) which reduce the soybean production.

The soil waterlogging is characterized by a hypoxia condition, low oxygen content, which occurs by the excess of water that fills the soil pore space. For the roots, this condition harms the respiration, dependent of oxygen, causing metabolic disorders (Garcia et al., 2020), related to the roots suberization, reducing the absorption of nutrients and water and changing the gas exchanges (Dalmolin et al., 2012). The hypoxia condition in soils also reduces the 1-aminocyclopropane-1-carboxylic acid production in the roots, inactive in anaerobic conditions, which is transported via xylem to the leaves where, in the presence of oxygen, is converted into ethylene (Fukao et al., 2019). The increase in the ethylene content in the tissues causes symptoms of plant senescence, such as the chlorotic aspect on the leaves, for increasing the activity of chlorophyllase and oxidase enzymes that degrade chlorophyll molecules (Taiz et al., 2017).

Due to changes caused in the gas exchanges and a reduction in the chlorophyll content, plants submitted to development in waterlogged soil normally present a reduction in the photosynthetic rate (Posso et al., 2018). This way, plants in waterlogged soil show metabolic changes that compromise both growth and yield.

The growth and productivity of soybean plants are also affected by the availability of solar radiation (Yang et al., 2018), because it directly influences the photosynthesis process. The reduced interception of solar radiation by leaves can reduce carbon sequestration and the production of assimilates destined to the growth and yield of plants. Thus, the interception of light in the reproductive phase is essential for high productivity of the crop, being that the restriction of light causes a reduction in production and accumulation of mass and int the production of soybeans (Yang et al., 2017).

Therefore, soybean plants simultaneously exposed to waterlogged soil and light restriction present physiological and biochemical changes that negatively affect the crop growth, development, and production.

In this context, the objective of this study was to investigate the chlorophyll content, foliar nutrient content, gas exchanges, plant height, dry matter accumulation and the grain production of soybean plants submitted to waterlogged soil and light restriction.

Materials and Methods

The study was carried in a randomized block design in a factorial scheme 2 × 2, with 6 repetitions in duplicate. The first factor was the presence and absence of waterlogged soil. The second factor was the presence and absence of light restriction on soybean plants. Treatments constituted of: plants conducted in waterlogged soil in full sun (waterlogged soil + without light restriction); plants conducted with regular irrigation and light restriction (without waterlogged soil + light restriction); plants conducted with waterlogged soil and light restriction (waterlogged soil + light restriction) and plants conducted with regular irrigation in full sun (soil with regular irrigation + without light restriction).

The experiment was implanted on December 15th using the soybean cultivar Bayer 2606® IPRO, which has the following characteristics: maturation group 6.0, medium size and indeterminate growth habit. For the study were kept two plants per pot, each one had a nominal capacity of 8.7 dm³, which were filled with soil from the A horizon of an Oxisol (Santos et al., 2018). The soil used as substrate had the following chemical characteristics in the 0-20 cm layer: P = 13.19 mg dm^{-3}; OM = 49.21 g dm^{-3}; pH ($CaCl_2$) = 6.37; H + Al = 2.54 cmol$_c$ dm^{-3}; Al^{+3} = 0 cmol$_c$ dm^{-3}; K^+ = 1.56 cmol$_c$ dm^{-3}; Ca^{2+} = 8.78 cmol$_c$ dm^{-3}; Mg^{2+} = 3.46 cmol$_c$ dm^{-3}; CEC = 16.34 cmol$_c$ dm^{-3}; V% = 84.46.

The soil used as substrate was fertilized using the recommendation for experiments in pots, supplying: 150 mg dm^{-3} of K as potassium chloride and 300 mg dm^{-3} of P as single superphosphate, which added 40 mg dm^{-3} of S and 85 mg dm^{-3} of Ca (Novaes et al., 1991).

All plants used in the experiment were conducted until the imposition of the treatments in full sun, being constantly monitored to ensure adequate development. For the maintenance of a satisfactory vegetal hydric status, daily irrigation regimes were performed to maintain the pots with humidity close to field capacity, until the imposition of the treatments.

The treatments with waterlogged soil were carried keeping the soil above the field capacity, being the pots immersed in a constant water blade of 0.15 m, in a 0.5 × 0.5 m and 0.2 m high wooden box covered with a plastic film. The pots immersed in the water blade were maintained with moisture above field capacity due to the phenomenon of capillarity that allowed the rise of water. To maintain the 0.15 m water line, water was replaced daily in the structure to prevent the soil from not being waterlogged. For the treatment's imposition with light restriction a wooden structure was used with the following dimensions: 1.5 × 1 m and 1.5 m high, being the structure made of 5.0 × 4.0 cm boards, covered with a shading cloth capable of retaining 80% of the solar radiation. Treatments were simultaneously imposed from the full bloom (R_2) stage and lasted for 30 days, until the beginning seed ($R_{5.2}$).

Gas exchanges were evaluated 20 days after the beginning of the treatments impositions, with the equipment Infra-Red Gas Analyzer (IRGA) Li-6400XT. These were made during the morning between 9:00 p.m. and 11:30 p.m., being determined on completely developed leaves, photosynthetically active and without injuries. The leaves were located in the plant medial third, which were identified before the treatments were imposed. It was determined: CO_2 liquid assimilation rate (A) (μmol CO_2 m^{-2} s^{-1}), transpiration rate (E) (μmol H_2O m^{-2} s^{-1}), and stomatal conductance (gs) (mol m^{-2} s^{-1}). It was also determined the chlorophyll relative content (SPAD index) with the portable device SPAD502-Plus Konica Minolta. Measurements were made on four fully expanded leaves from each of the two plants in each pot, obtaining an average value.

Biometric evaluations were made at 30 days after the experiment was implanted. It was determined plant height (PH) expressed in centimeters (cm). Next the plants were sectioned into aerial part and root system, being the samples placed into kraft paper bags and put to dry in an air forced circulation oven at 65 °C for 72 h. The material was weighed on a chapel type analytical scale, determining the aerial dry matter (ADM) and root dry matter (RDM), expressed in grams (g).

At 30 days after the treatments were imposed, leaf samples were also collected, diagnoses leaf, for the determination of macronutrients in the foliar tissues. For this, half of the foliar samples were submitted to the Kejdahl method for the determination of nitrogen, phosphorus, and potassium content, expressed in g kg^{-1} of dry matter (Silva, 2009). The other half of the foliar samples were submitted to the dry digestion method for the determination of calcium and magnesium, expressed in g kg^{-1} of dry matter (Silva, 2009).

At the end of the plant cycle the soybean production components and the production per plant were determined, then determining the number of pods per plant (NPP). Next the grains were collected and their mass was determined, providing the data of grain production per plant (PRODP), expressed in grams (g), correcting the moisture content to 13% according to the methodology of Marcos Filho (2015). For the one hundred grain mass (OGM) a sample of each experimental plot was separated, where 4 repetitions of 25 grains were counted and the mass of one hundred grains was subsequently determined.

Data were submitted to analysis of variance ($p < 0.05$) and compared by the Tukey test ($p < 0.05$), using the SISVAR 5.1 software (Ferreira, 2014).

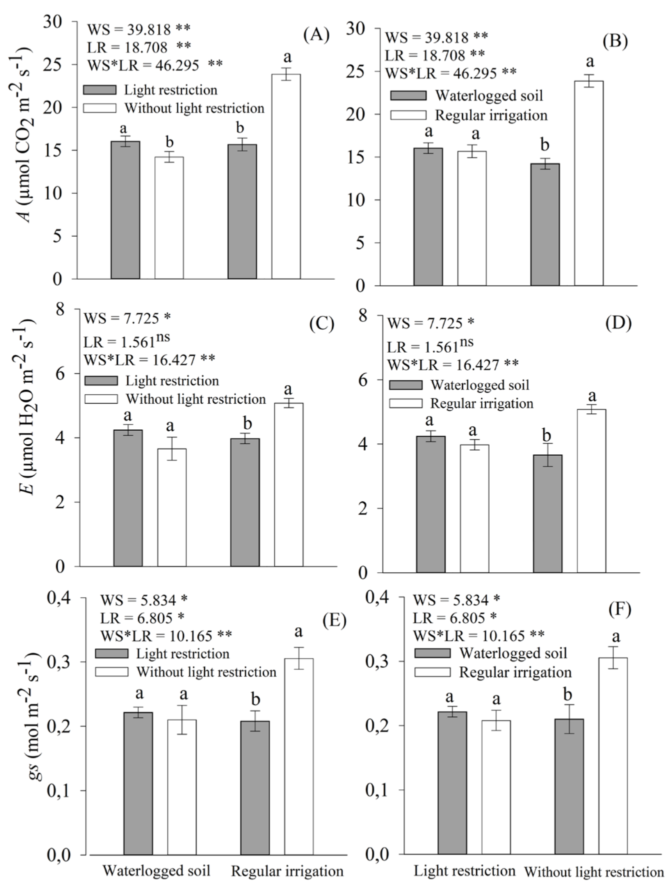
Results and Discussion

Foliar gas exchanges and chlorophyll relative content

The soybean development in waterlogged soil condition and light restriction, from the full bloom (R_2), negatively affected the gas exchanges, with a significant effect for the interaction between the factors presence and absence of waterlogged soil and presence and absence of light restriction in the plants for the CO_2 liquid assimilation rate (A), transpiration (E), and stomatal conductance (gs) (Figure 1).

In Figure 1 are presented the data for the gas exchange readings carried 20 days after the treatments were imposed. The results show that plants submitted to regular irrigation and light restriction presented a reduction of A, E, and gs in the order of 34.0, 22.0, and 32.0%, respectively, when compared to the plants cultivated with regular irrigation in full sun. For plants conducted in waterlogged soil in full sun it was also observed reduction of A, E, and gs in the order of 40.0, 28.0, and 31.0%, respectively, when compared to plants cultivated under regular irrigation and full sun. For the plants conducted in waterlogged soil, those in full sun presented an inferior value for A of 11.0%, compared to plants cultivated with light restriction (Figure 1A and 1B).

For plants under waterlogged soil condition in full sun, the existent changes in the gas exchanges are related to the low oxygen content available to the root system. To explain this relationship, it is necessary to highlight that under hypoxia, low oxygen concentration, the suberization or lignification of the root may and a low activity of aquaporins may occur (Aroca et al., 2012) which reduces the capacity of absorbing water. Thus, roots in hypoxia condition present lower hydraulic conductivity, reducing the water potential in the plant. The smaller water potential in the plant provides a higher production of abscisic acid in the roots and, consequently,



The columns followed by similar lower case letters do not differ by Tukey test with a 5% probability. The calculated F values followed by * ($p < 0.05$); ** ($p < 0.01$); ns not significant. The bars in the columns represent the standard error of the average.

Figure 1. CO_2 liquid assimilation rate (A) and (B), transpiration rate (C) and (D), and stomatal conductance (E) and (F) of soybean plants cultivar Bayer 2606® IPRO. The data was obtained 20 days after the treatments were imposed referent to the presence and absence of factors waterlogged soil (WS) and light retriction (LR).

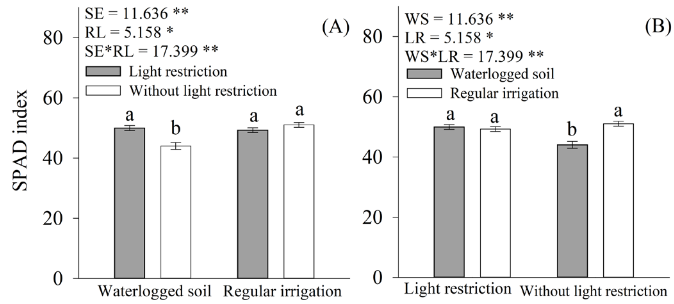
increase its content in the leaves promoting the stomatal closure (Bashar et al., 2019), even though the leaves present no turgor loss.

Thus, the hypoxia state of the root tissue conditions both metabolic and morphological changes that alter water relations in plants, resulting in a less stomatal opening which may be the cause of the reduction of E observed in this study of plants submitted to waterlogged soil in full sun in relation to plants with regular irrigation in full sun. In the hypoxia condition, reductions in the stomatal opening may be a survival mechanism, in view of the need to reduce water loss through transpiration, since water absorption is impaired (Dalmolin et al., 2012). However, the reduction in the stomatal opening, with consequent reduction of transpiration, to maintain satisfactory water status, results in less CO_2 diffusion through stomata which reduces the photosynthetic rate (Ploschuk et al., 2018), a common response for plants with the root system exposed to the waterlogged soil condition (Posso et al., 2018). These statements are confirmed with the reduction of A found in this study for plants in waterlogged soil condition in full sun.

For plants in waterlogged soil in full sun, the decrease of A is also associated with the reduction in the chlorophyll relative content in the leaves (SPAD index). At 20 days after the treatments were imposed, the plants exposed to the waterlogged soil condition and full sun presented a chlorotic aspect and consequently a reduction in the SPAD values of 14.0 and 13.0% in relation to plants conducted with regular irrigation without light restriction and plants conducted under waterlogged soil and light restriction, respectively (Figure 2).

The chlorotic aspect of the leaves of plants submitted to the waterlogged soil condition in full sun may be associated with a depletion of oxygen content in the tissues of the roots conducted on waterlogged soil, which stimulates the production of 1-aminocyclopropane-1-carboxylic acid, an ethylene precursor (Bashar et al., 2019). Posteriorly this precursor is transported to the aerial part, where in the presence of oxygen is converted to ethylene (Fukao et al., 2019). The increase in the ethylene concentration in the leaf tissues stimulates the greater activity of chlorophyllase and oxidase enzymes that degrade chlorophyll molecules (Taiz et al., 2017). Associated with it is the increase in the production of oxygen reactive species (Posso et al., 2018) which also promote the degradation of chlorophyll molecules, turning the leaves into chlorotic. This way, due to the chlorophyll molecules being directly responsible for the photosynthesis, in hypoxia condition, probably this is the main cause of the reduction on the CO_2 assimilation (Garcia et al., 2020).

Still for plants conducted under waterlogged soil condition, those exposed to light restriction presented higher A and SPAD index, discording from the results found by Dalmolin et al. (2012) in study with *Vochysia divergens*, a plant adapted to the development in environments with low luminosity, in the presence and absence of the factors waterlogged soil and light restriction. According to the authors, plants in waterlogged soil condition, with light restriction or in full sun, presented chlorotic leaves and higher losses in the liquid photosynthesis



The columns followed by similar lower case letters do not differ by Tukey test with a 5% probability. The calculated F values followed by * ($p < 0.05$); ** ($p < 0.01$); ^{ns} not significant. The bars in the columns represent the standard error of the average.

Figure 2. Chlorophyll relative content (SPAD index) (A and B) of soybean plants cultivar Bayer 2606® IPRO. The data was obtained 20 days after the treatments were imposed referent to the presence and absence of factors waterlogged soil (WS) and light retriction (LR).

in comparison to plants with regular irrigation with the presence of shading.

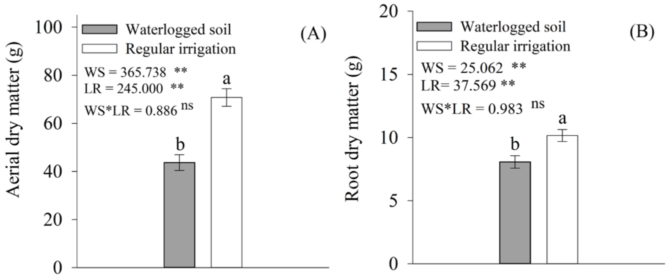
For plants conducted under light restriction, the reduction observed for A, E, and gs may be explained by the lower photosynthetically active photon flux density (PPFD). The photosynthetic processes are very sensitive to the low availability of photosynthetically active radiation (Yang et al., 2018). With this, it is observed that the average PFFD on the treatments with light restriction and in full sun during the evaluation were 362.86 μmol m^{-2} s^{-1} and 1,623.73 μmol m^{-2} s^{-1}, respectively, with a reduction of 78.0% in the PFFD inside the structures with shading cloth.

Su et al. (2014) found similar results studying the effect of shading on soybean plants cultivated in intercropped with corn. In this study the soybean canopy intercepted 50.0% less photosynthetically active radiation in relation to the corn plant canopy. According to the authors, the shading caused by the corn in the soybean plants caused a reduction of A, E, and gs in the order of 38.0, 43.0, and 55.0%, respectively, being in accordance to the results found in this study.

It can then be said that the data indicate that soybean plants exposed to the conditions of waterlogged soil and light restriction, for a 20-day period from the full bloom (R_2), presented variations on the gas exchanges, with reduction of the photosynthesis. However, for plants under waterlogged soil condition, the light restriction seems to attenuate the negative effects from the hypoxia, with no apparent symptoms of chlorosis in the leaves and minor drops in net CO_2 assimilation.

Biometric analysis and nutrient foliar content

The 30-day period of development of soybean plants in waterlogged soil from the full bloom (R_2) resulted in negative effects on the accumulation of dry matter. In Figure 3 are shown the results referent to the treatment's averages with waterlogged soil and regular irrigation. The development in waterlogged soil in the reproductive phase caused a reduction in the accumulation of both aerial dry matter (ADM) and root dry matter (RDM) in the order of 38.0 and 20.0%, respectively, when compared to plants with regular irrigation.



The columns followed by similar lower case letters do not differ by Tukey test with a 5% probability. The calculated F values followed by * ($p < 0.05$); ** ($p < 0.01$); ns not significant. The bars in the columns represent the standard error of the average.

Figure 3. Aerial dry matter (A) and root dry matter (B) of soybean plants cultivar Bayer 2606® IPRO. Values are averages of treatments with waterlogged soil and regular irrigation, obtained 30 days after the imposition of treatments referring to the presence and absence of soaked soil factors waterlogged soil (WS) and light retriction (LR).

In plants subjected to waterlogged soil condition a reduction on the photosynthetic rate occurs and, consequently, there is a decrease in the photoassimilates used during the plant's development (Barickman et al., 2019). However, other events associated with the hypoxia condition also help to explain the reduction in the dry matter accumulation, for example the oxygen depletion, that drastically reduces the production of metabolic energy destined to the root system maintenance. For the maintenance of the metabolic activity of the root tissues the metabolism becomes anaerobic (Borella et al., 2017).

It is still worth highlight that, in the anaerobic route, which is less efficient in the production of energy, occurs the production of high amounts of pyruvate, which is converted into acetaldehyde and lactic acid, toxic compounds when in high concentrations in plants, capable of causing lesions in the leaf and root tissues (Zhang et al., 2017). In addition, plants developing with their root system in a state of hypoxia also present increased production of free radicals that also cause damage to leaf and root tissues (Wang et al., 2017). In the present study damages in the root tissues were observed, with the presence of a necrosed tissue, which may be one of the causes of the reduction in the root dry matter accumulation.

The growth and development of plants conducted in waterlogged soil may also be negatively affected by the reduction in the membrane permeability of tissues exposed to the waterlogged soil condition (Aroca et al., 2012), causing a reduction in the absorption of ions in the root tissues. Besides, plants with the root system in a state of hypoxia present reduction in the production of ATP and consequently, reduction in the active absorption of nutrients (Marashi, 2018). The smaller capacity of ions absorption of the root tissues in hypoxia condition reduces the nutrient content in the aerial part of plants cultivated in waterlogged soil, such as nitrogen, phosphorus, potassium, and magnesium (Sharma et al., 2018) and, consequently, contributes to the reduction in the soybean growth and dry matter accumulation.

This discussion is confirmed for plants conducted on waterlogged soil in full sun, because they presented a reduced foliar content of nitrogen, phosphorus, potassium, and magnesium. However, for plants in waterlogged soil with the presence of shading the nutrients foliar content were not affected (Table 1).

One explanation for this result, although speculative, is the possibility that there was less dilution of nutrients in the tissues of the aerial part of the plants conducted in waterlogged soil and the presence of light restriction in relation to the plants in waterlogged soil in full sun. To comprehend this possible relationship, it is observed that plants conducted in waterlogged soil and the presence of light restriction and plants in waterlogged soil in full sun presented aerial dry matter averages of 32.5 ± 3.4 and 54.1 ± 3.22 g, respectively. Thus, this condition may have provided less dilution of nutrients in the aerial part and, consequently, avoided the reduction of the foliar content of nutrient evaluated in plants conducted in waterlogged soil with the presence of light restriction.

Data presented in Table 1 show that plants in waterlogged soil and full sun presented reduced nitrogen, phosphorus, potassium and magnesium content in the order of 43.0, 32.0, 22.0, and 65.0%, respectively, when compared to plants cultivated with regular irrigation in full sun. For plants in waterlogged soil in full sun it was also observed a lower content of nitrogen, phosphorus, potassium and magnesium in the order of 44.0, 38.0, 21.0, and 65.0%, respectively, when

Table 1. Foliar content of nutrients in soybean leaves (g kg^{-1}) cultivar Bayer 2606® IPRO. The data were obtained 30 days after full bloom (R_2), when the treatments related to the presence and absence of waterlogged soil (WS) and light restriction (LR) factors were imposed, in the municipality of Marechal Cândido Rondon, PR, Brazil, 2018/2019 (1).

WS	Nitrogen		Phosphorus		Potassium		Magnesium		Calcium	
	LR									
	With	Without	With	Without	With	Without	With	Without	With	Without
With	52.30Aa	29.67Bb	5.54Aa	3.31Bb	17.66Aa	13.10Bb	4.49Aa	1.72Bb	20.18ns	18.81ns
Without	53.41Aa	51.94Aa	5.37Aa	4.96Aa	17.74Aa	18.11Aa	4.42Aa	4.38Aa	17.77ns	18.49ns
S(2)	40-54		2.5-5		17-25		3-10		4-20	
CV (%)	11.59		13.48		3.77		19.08		11.97	
WL(3)	819.82**		7.828*		62.00**		19.84**		2.22ns	
LR(3)	871.10**		25.14**		37.67**		23.55**		0.123ns	
WS*LR(3)	671.30**		11.84**		57.35**		21.44**		1.30ns	

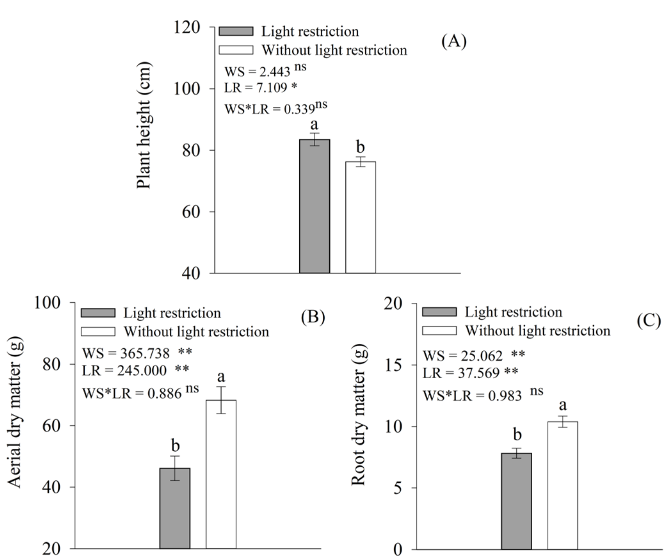
(1) Averages followed by similar uppercase letters in the row and lowercase letters in the column, do not differ by Tukey test at 5% probability. (2) Sufficient nutrient content according to Silva (2009). (3) The calculated F values followed by * ($p < 0.05$); ** ($p < 0.01$); ns not significant.

compared to plants cultivated with regular irrigation and light restriction. In addition, plants in waterlogged soil in full sun present foliar content of nitrogen, potassium and magnesium lower than the sufficiency levels for soybean (Silva, 2009), corroborating for the reduction in the accumulation of dry matter observed in the study.

The 30-day period of development under light restriction from the full bloom (R_2) also negatively affected the soybean dry matter accumulation. In Figure 4 are shown the average results of the treatments with presence and restriction of light and in full sun, in which plants submitted to the light restriction presented a reduction of ADM and RDM of 32.0 and 23.0%, respectively when compared to plants in full sun. However, the exposition to light restriction provided a 10.0% increase in plant height (PH) in relation to plants in full sun (Figure 4A).

The increase in PH of plants conducted under light restriction is related to changes in the hormonal balance. The smallest interception of solar radiation results in smaller auxin degradation in the plant's apex, causing a strong apical dominance (Taiz et al., 2017). Wu et al. (2016) demonstrated that soybean plants under shading condition, with less interception of solar radiation, had greater apical dominance, leading to the lengthening of internodes and, consequently, greater plant height, corroborating the results of the present study.

In soybean plants conducted under light restriction, a reduction in the CO_2 liquid assimilation rate occurs (Fan et al., 2018) causing less production of photoassimilates destined to the plant growth, contributing to reduce the ADM and RDM as observed in this study. The lower carbon liquid assimilation observed in plants conducted under light restriction is explained by the sensitivity of the photosynthetic apparatus to the decline in the interception of active photosynthetic radiation (Yang et al., 2018). Thus, the smaller dry matter accumulation in plants with low luminosity may be attributed to the reduction in the production of photoassimilates.



The columns followed by similar lower case letters do not differ by Tukey test with a 5% probability. The calculated F values followed by * ($p < 0.05$); ** ($p < 0.01$); ns not significant. The bars in the columns represent the standard error of the average.

Figure 4. Plant height (A), aerial dry matter (B) and root dry matter (C) of soybean plants cultivar Bayer 2606® IPRO. Values are averages obtained 30 days after the imposition of treatments referring to the presence and absence of light restriction.

Similar result was observed by Su et al. (2014), in a study that evaluated the effect of light restriction in soybean plants grown intercropped with corn. In the study carried by these authors, the canopy of soybean intercepted only 50% of the active photosynthetic radiation intercepted by the canopy of corn plants. According to the authors, this condition caused reduction of 78.7% on the soybean biomass cultivated intercropped with corn in relation to soybean plants in full sun. Wu et al. (2016) also demonstrated that soybean plants with less interception of photosynthetically active radiation have reduced phytomass production due to less carbon fixation.

Production components and production per plant

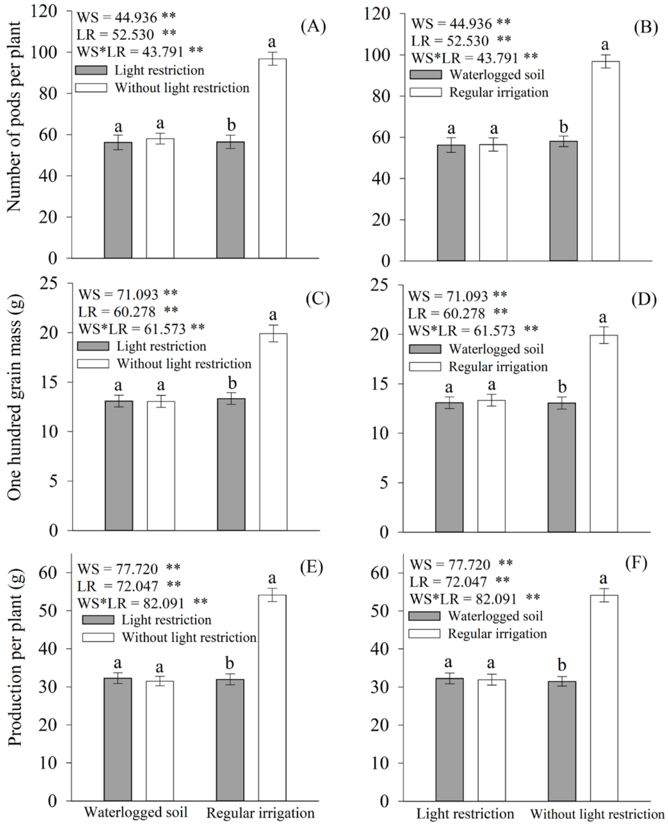
The 30-day period of the soybean development under waterlogged soil condition and light restriction, from the full bloom (R_2), negatively influenced the grain production, with a significant effect of interaction between the presence and absence of waterlogged soil and presence and absence of light restriction, for the production components and production per plant (Figure 5).

For plants submitted to the regular irrigation and light restriction, there was a reduction in the number of pods per plant (NPP), one hundred grain mass (OGM) and production per plant (PRODP) in the order of 42.0, 33.0, and 41.0%, respectively, when compared to plants submitted to regular irrigation in full sun. Plants conducted in waterlogged soil in full sun also presented reduction for NPP, OGM and PRODP in the order of 40.0, 34.0, and 42.0%, respectively, when compared to plants under regular irrigation in full sun (Figure 5).

Beutler et al. (2014) found similar results to the ones in this study, where the development of soybean plants in waterlogged soil conditions, from the phenological stage R_2, resulted in a 41.0% reduction in the grain yield, associated to lower grain mass and smaller number of pods per plant.

For plants under regular irrigation and light restriction, the reduction of NPP, OGM and PRODP is associated with less interception of photosynthetically active radiation. The smaller interception of photosynthetically active photons by soybean plants causes a reduction in the carbon liquid assimilation and, consequently, a reduction in the production components, such as number of pods per plant, number and average grain mass, reducing the production due to the smaller photosynthetic rate (Yang et al. 2017). This discussion is confirmed by the reduction of carbon assimilation found in this study.

For plants submitted to waterlogged soil condition and light restriction, no significant difference was observed for NPP, OGM, and PRODP when compared to plants submitted to waterlogged soil in full sun and plants submitted to regular irrigation in light restriction (Figure 5). Thus, it is observed that plants simultaneously submitted to the environmental stresses



The columns followed by similar lower case letters do not differ by Tukey test with a 5% probability. The calculated F values followed by * ($p < 0.05$); ** ($p < 0.01$); ^{ns} not significant. The bars in the columns represent the standard error of the average.

Figure 5. Number of pods per plant (A) and (B), one hundred grain mass (C) and (D), and production per plant (E) and (F) of soybean plants cultivar Bayer 2606® IPRO. The data was obtained 20 days after the treatments were imposed referent to the presence and absence of factors waterlogged soil (WS) and light retriction (LR).

waterlogged soil and light restriction, seems to acclimate, resulting from the interaction between the waterlogged soil and light restriction conditions, preventing the reduction of the production of components from adding up to the isolated effects of the stresses studied.

In plants, there is a gradual increase in the demand for photoassimilates from the vegetative to the reproductive stage, reaching the highest photosynthetic demand in the period that comprehend the full bloom up to the beginning seed. Thus, it is observed that the PRODP in the present study is positively correlated to the CO_2 liquid assimilation rate ($r = 0.93$; $p < 0.05$) determined 20 days after the environmental stresses were imposed. The positive correlation between PRODP and A helps to explain the similar behavior of grain production of plants exposed to conditions of waterlogged soil and/or light restriction when compared among themselves. Besides corroborating for the higher grain production in plants from the treatment without stress, that presented higher CO_2 liquid assimilation rate in this study.

To increase the understanding of the negative effects generated by exposure to waterlogged soil conditions and/or light restriction, there is a need for further studies. It is important to conduct studies to evaluate the effects of exposure to stressful conditions at different phenological stages and for different periods of time.

Conclusions

For soybean crops, the incidence of environmental stress, waterlogging of the soil and light restriction, alone or together, in the reproductive phase, provide less stomatal conductance, transpiration and liquid photosynthesis compared to plants in the stress-free condition.

Soybean plants in waterlogging soil condition in full sun presented chlorotic leaves with less contents of nitrogen, phosphorus, potassium and magnesium in relation to plants from the other treatments.

Soybean plants exposed to development in waterlogged soil presented smaller mass accumulation. For soybean plants under light restriction a reduction in the dry matter accumulation occurs, associated to the plant's etiolation.

The production of grains of soybean and grain production of plants exposed to the environmental stresses waterlogged soil and light restriction in a conjunct way or isolate are similar among themselves and inferior to plants without stress.

The damage to the metabolism of soybean plants grown under waterlogged soil and/or light restriction conditions for a period of thirty days from full flowering (R_2) causes a reduction in carbon assimilation that is related to a decline in dry mass accumulation and grain yield.

Acknowledgment

This study was financed in part by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES).

Compliance with Ethical Standards

Author contributions: Conceptualization: RCJ, VFG; Data curation: RCJ, VFG, LGB; Formal analysis: RCJ, ADS, ODCB; Funding acquisition: VFG; Investigation: RCJ, TSB, ODCB; Methodology: RCJ, LGB, TSB; Project administration: RCJ; Resources: VFG; Software: No programs were developed; Supervision: VFG; Validation: RCJ, VFG; Visualization: RCJ, ADS; Writing – original draft: RCJ, VFG; Writing – review & editing: RCJ, VFG, TSB, ADS, ODCB, LGB.

Conflict of interest: The authors declare no conflict of interest.

Funding source: The Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES) – Finance Code 001.

Literature Cited

Aroca, R.; Porcel, R.; Ruiz-Lozano, J. M. Regulation of root water uptake under abiotic stress conditions. Journal of Experimental Botany, v.61, n.1, p.47-57, 2012. https://doi.org/10.1093/jxb/err266.

Barickman, T.C.; Simpson, C.R.; Sams, C.E. Waterlogging causes early modification in the physiological performance, carotenoids, chlorophylls, proline, and soluble sugars of cucumber plants. Plants, v.8, n.160, p.1-15, 2019. https://doi.org/10.3390/plants8060160.

Bashar, K.K.; Tareq, M.Z.; Amin, M.R.; Honi, U.; Ul-Arif, M.T.; Sadat, M.A.; Mosaddeque Hossen, Q.M. Phytohormone-mediated stomatal response, escape and quiescence strategies in plants under flooding stress. Agronomy, v.9, n.2, p.1-13, 2019. https://doi.org/10.3390/agronomy9020043.

Beutler, A.N.; Giacomeli, R.; Alberto, C. M.; Silva, V.N.; da Silva Neto, G.F.; Machado, G.A.; Santos, A.T.L. Soil hydric excess and soybean yield and development in Brazil. Australian Journal of Crop Science, v.8, n.10, p.1461-1466, 2014. http://www.cropj.com/beutler_8_10_2014_1461_1466.pdf. 06 May. 2021.

Borella, J.; Oliveira, H.C.; de Oliveira, D.S.C.; Braga, E.J.B.; Oliveira, A.C.B.; Sodek, L.; Amarante, L. Hypoxia-driven changes in glycolytic and tricarboxylic acid cycle metabolites of two nodulated soybean genotypes. Environmental and Experimental Botany, v.133, n.1, p.118-127, 2017. https://doi.org/10.1016/j.envexpbot.2016.10.007.

Dalmolin, Â.C.; Dalmagro, H.J.; Lobo, F. de A.; Antunes Junior, M.Z.; Ortíz, C.E.R.; Vourlitis, G. L. Effects of flooding and shading on growth and gas exchange of *Vochysia divergens* Pohl (Vochysiaceae) of invasive species in the Brazilian Pantanal. Brazilian Journal of Plant Physiology, v.24, n.2, p.74-84, 2012. https://doi.org/10.1590/S1677-04202012000200001.

Fan, Y.; Chen, J.; Cheng, Y.; Raza, M.A.; Wu, X.; Wang, Z.; Yang, F. Effect of shading and light recovery on the growth, leaf structure, and photosynthetic performance of soybean in a maize-soybean relay-strip intercropping system. PLoS ONE, v.13, n.5, e0198159, 2018. https://doi.org/10.1371/journal.pone.0198159.

Ferreira, D.F. Sisvar: a guide for its bootstrap procedures in multiple comparisons. Ciência e Agrotecnologia, v.38, n.2, p.109-112, 2014. https://doi.org/10.1590/S1413-70542014000200001.

Fukao, T.; Barrera-Figueroa, B.E.; Juntawong, P.; Peña-Castro, J.M. Submergence and waterlogging stress in plants: A review highlighting research opportunities and understudied aspects. Frontiers in Plant Science, v.10, e00340, 2019. https://doi.org/10.3389/fpls.2019.00340.

Garcia, N.; da-Silva, C.J.; Cocco, K.L.T.; Pomagualli, D.; Oliveira, F.K.; Silva, J.V.L.; Amarante, L. Waterlogging tolerance of five soybean genotypes through different physiological and biochemical mechanisms. Environmental and Experimental Botany, v.172, e103975, 2020. https://doi.org/10.1016/j.envexpbot.2020.103975.

Marashi, S.K. Evaluation of uptake rate and distribution of nutrient ions in wheat (*Triticum aestivum* L.) under waterlogging condition. Iranian Journal of Plant Physiology, v.8, n.4, p.2539-2547, 2018. https://ijpp.iau-saveh.ac.ir/article_543416_9759af0675f4b95ccff15ac7272cbd50.pdf. 06 May. 2021.

Marcos Filho, J. Fisiologia de Sementes de Plantas Cultivadas. Londrina: Abrates, 2015. 659p.

Novaes, R.F. de, Neves, J.C.L.; Barros, N.F. de. Ensaio em ambiente controlado. In Oliveira, A.J.; Garrido, W.E.; Araujo, J.D.; Lourenço, S. (Orgs.). Métodos de pesquisa em fertilidade do solo. Brasília: Embrapa, 1991. p.189-253.

Ploschuk, R.A.; Miralles, D.J.; Colmer, T.D.; Ploschuk, E.L.; Striker, G.G. Waterlogging of winter crops at early and late stages: Impacts on leaf physiology, growth and yield. Frontiers in Plant Science, v.9, e01863, 2018. https://doi.org/10.3389/fpls.2018.01863.

Posso, D.A.; Borella, J.; Reissig, G.N.; Bacarin, M.A. Root flooding-induced changes in the dynamic dissipation of the photosynthetic energy of common bean plants. Acta Physiologiae Plantarum, v.150, n.1, e212, 2018. https://doi.org/10.1007/s11738-018-2790-9.

Santos, H.G.; Jacomine, P.K.T.; Anjos, I.H.C.; Oliveira, V.A.; Lumbreras, J.F.; Coelho, M.R.; Almeida, L.A.; Araújo Filho, J.C.; Oliveira, J.B.; Cunha, T.J.F. Sistema brasileiro de classificação de solos. 5.ed. Brasília: Embrapa Solos, 2018. 356p.

Sharma, S.K.; Kulshreshtha, N.; Kumar, A.; Yaduvanshi, N.P.S.; Singh, M.; Prasad, K. R.K.; Basak, N. Waterlogging effects on elemental composition of wheat genotypes in sodic soils. Journal of Plant Nutrition, v.41, n.10, p.1252-1262, 2018. https://doi.org/10.1080/01904167.2018.1434541.

Silva, F.C. da. Manual de análises químicas de solos, plantas e fertilizantes. Brasília: Embrapa Informação Tecnológica, 2009. 627p.

Su, B.Y.; Song, Y.X.; Song, C.; Cui, L.; Yong, T.W.; Yang, W.Y. Growth and photosynthetic responses of soybean seedlings to maize shading in relay intercropping system in Southwest China. Photosynthetica, v.52, n.3, p.3, 332-340, 2014. https://doi.org/10.1007/s11099-014-0036-7.

Taiz, L.; Zeiger, E.; Moller, I. M.; Murphy, A. Fisiologia e desenvolvimento vegetal. Porto Alegre: Artmed, 2017. 858p.

Wang, F.; Chen, Z.H.; Shabala, S. Hypoxia sensing in plants: on a quest for ion channels as putative oxygen sensors. Plant and Cell Physiology, v.58, n.7, p.1126-1142, 2017. https://doi.org/10.1093/pcp/pcx079.

Wu, Y.; Gong, W.; Yang, F.; Wang, X.; Yong, T. Yang, W. Responses to shade and subsequent recovery of soya bean in maize-soya bean relay strip intercropping. Plant Production Science, v.19, n.2, p.206-214, 2016. https://doi.org/10.1080/1343943X.2015.1128095.

Yang, F.; Feng, L.; Liu, Q.; Wu, X.; Fan, Y.; Raza, M.A.; Yang, W. Effect of interactions between light intensity and red-to- far-red ratio on the photosynthesis of soybean leaves under shade condition. Environmental and Experimental Botany, v.150, p.79-87, 2018. https://doi.org/10.1016/j.envexpbot.2018.03.008.

Yang, F.; Liao, D.; Wu, X.; Gao, R.; Fan, Y.; Raza, M.A.; Yang, W. Effect of aboveground and belowground interactions on the intercrop yields in maize-soybean relay intercropping systems. Field Crops Research, v.203, p.16-23, 2017. https://doi.org/10.1016/j.fcr.2016.12.007.

Zhang, P.; Lyu, D.; Jia, L.; He, J.; Qin, S. Physiological and de novo transcriptome analysis of the fermentation mechanism of *Cerasus sachalinensis* roots in response to short-term waterlogging. BMC Genomics, v.18, e649, 2017. https://doi.org/10.1186/s12864-017-4055-1.