

Gas exchanges and chlorophyll fluorescence of soybean genotypes subjected to flooding stress

Trocas gasosas e fluorescência de clorofila de genótipos de soja submetidos a estresse por alagamento

Silvana F. da Silva¹, Marcio de O. Martins², Paulo V. A. das Chagas², Gisele L. dos Santos¹, Ester dos S. Coêlho¹, Aurélio P. Barros Júnior¹, Lindomar M. da Silveira¹, João E. da S. Ribeiro^{1*}

¹Department of Agronomic and Forest Sciences, Universidade Federal Rural do Semi-Árido, Mossoró, RN, Brazil. ²Center for Biological and Natural Sciences, Universidade Federal do Acre, Rio Branco, AC, Brazil.

ABSTRACT - The objective of this work was to evaluate the ecophysiological responses of soybean subjected to soil flooding. The experiment was conducted in a completely randomized design with five replications. A 3 x 3 factorial scheme was used, consisting of three soybean genotypes (tolerant, sensitive and a commercial cultivar), and three water conditions (control treatment – soil was maintained at 70% of field capacity throughout the plant cycle; soil flooding for 10 days in the vegetative period + 10 days in the reproductive period; and soil flooding for 10 days only in the reproductive period). Three evaluations were carried out regarding chlorophyll fluorescence and gas exchange: after flooding in the vegetative period (V2); after flooding in the reproductive period (R2), and ten days after draining the water. Tolerant genotypes and sensitive genotypes experienced reductions in photosynthetic rate and stomatal conductance when subjected to water stress in the reproductive stage. However, under stress in the vegetative stage, only the tolerant and sensitive genotypes reduced the actual quantum efficiency and electron transport rate, and at the moment of flooding in the reproductive stage, all had changes and did not show recovery for these variables. As for non-photochemical quenching, only the sensitive genotype increased the rate, under stress in stages V2/R2 and R2. The local commercial cultivar is more adapted to soil flooding conditions, as it shows better physiological responses to adapt to soil flooding conditions.

Keywords: *Glycine max* (L.) Merr. Water stress. Abiotic stress. Water use efficiency.

Conflict of interest: The authors declare no conflict of interest related to the publication of this manuscript.



This work is licensed under a Creative Commons Attribution-CC-BY <https://creativecommons.org/licenses/by/4.0/>

Received for publication in: January 22, 2024.
Accepted in: March 20, 2024.

***Corresponding author:**
<j.everthon@hotmail.com>

RESUMO - O objetivo deste trabalho foi avaliar as respostas ecofisiológicas de soja submetida ao alagamento do solo. O experimento foi conduzido em delineamento inteiramente casualizado com cinco repetições. Foi utilizado um esquema fatorial 3 x 3, composto por três genótipos de soja (tolerante, sensível e uma cultivar comercial); e três condições hídricas (tratamento controle – solo foi mantido a 70% da capacidade de campo 11 durante todo o ciclo da planta; alagamento do solo por 10 dias no período vegetativo + 10 dias no 12º período reprodutivo; e alagamento do solo por 10 dias apenas no período reprodutivo período. Foram realizadas três avaliações quanto à fluorescência da clorofila a trocas gasosas: após a inundação do período vegetativo (V2); após o alagamento do período reprodutivo (R2), e dez dias após a drenagem da água. Os genótipos tolerantes e sensíveis sofreram redução na taxa fotossintética e na condutância estomática quando submetidos ao estresse hídrico na fase reprodutiva. Porém, sob estresse na fase vegetativa, apenas os genótipos tolerantes e sensíveis reduziram a eficiência quântica atual e a taxa de transporte de elétrons, e no momento do alagamento na fase reprodutiva, todos sofreram alterações e não apresentaram recuperação para essas variáveis. Quanto à quenching não fotoquímico, apenas a sensível aumentou a taxa, nas tensões nos estágios V2/R2 e R2. A cultivar comercial local é mais adaptada às condições de alagamento do solo, pois apresenta melhores respostas fisiológicas de adaptação às condições de alagamento do solo.

Palavras-chave: *Glycine max* (L.) Merr. Estresse hídrico. Estresse abiótico. Eficiência no uso da água.

INTRODUCTION

The Amazon Region has a climate distributed in such a way as to characterize two distinct seasons: the dry and the rainy season, with total rainfall ranging from 1,400 to 3,500 mm per year. The two climatic extremes are not favorable for agricultural production, the first is probably the greatest limiting factor for the development of agriculture and the second is also a limiting and worrying factor for food production, as it affects the ability of plants to grow and develop, which can lead to death due to anoxia (ZAHRA et al., 2021).

Due to population growth, climate change, soil degradation and pollution, the current area of arable land is decreasing, given the great pressure on the global food supply, resulting in the entry of agricultural crops in previously unexplored regions, such as in the north of Brazil (MOURTZINIS; CONLEY, 2017). The exploration of flooded areas with species of economic importance depends on the identification of plants that can not only survive soil flooding, but also provide yields capable of bringing economic return; thus, the soybean crop appears to be an excellent alternative (KAUR et al., 2020).

Soybean [*Glycine max* (L.) Merr.] is a species considered sensitive to

excess water in the soil, and flood conditions can result in under development of the plant, low yield and grain quality, and even death. Soybean production under flooding could be sustained by developing flood-tolerant cultivars through breeding programs (ZHOU et al., 2021). The hypoxia or anoxia experienced by the root system alters cellular metabolism, causing an immediate drop in plant root respiration (LIAO; LIN, 2001). When the soil becomes hypoxic, due to flooding, the roots are subjected to a stress condition and, thus, the plants respond with greater or lesser efficiency, allowing the distinction of tolerant and intolerant species and/or cultivars (DANIEL; HARTMAN, 2024).

Excessive rainfall can lead to waterlogging of the soil, which generates different impacts on plants, with some species dying quickly, while others are able to acclimatize and survive under such conditions (ZHOU et al., 2020; HONÓRIO et al., 2021). Flood stress reduces the oxygen supply to submerged plant tissues, so plants employ strategies to compensate for anaerobic soil conditions (WITTMANN et al., 2013; NAKAMURA; NOGUCHI, 2020).

In general, plants show a variety of morphophysiological responses to deal with prolonged periods of flooding, such as the development of adventitious roots, hypertrophied aerenchyma and lenticels, reduced gas exchange and increased carbohydrate reserves in the roots (PIMENTEL et al., 2014; ARGUS; COLMER; GRIERSON, 2015; MARCÍLIO et al., 2019; LEÓN; CASTILLO; GAYUBAS, 2020; LORETI; PERATA, 2020). An early response to waterlogging, especially in sensitive crop species such as soybean, is the reduction of water absorption by the root system, triggering several changes in the plant. The objective of this work was to evaluate the ecophysiological responses of soybean subjected to soil flooding.

MATERIAL AND METHODS

The experiment was carried out in the experimental garden of the Federal University of Acre (UFAC), located in the city of Rio Branco, Acre, Brazil (9°53'16"S, 67°49'11"W), from November 2020 to February 2021.

The experiment was conducted in a completely randomized design with five replications. A 3 x 3 factorial scheme was used, consisting of three soybean genotypes (tolerant, sensitive and a commercial cultivar), and three water conditions (control treatment – soil was maintained at 70% of field capacity throughout the plant cycle; soil flooding for 10 days in the vegetative period + 10 days in the reproductive period; and soil flooding for 10 days only in the reproductive period).

Three contrasting soybean genotypes in relation to soil waterlogging tolerance were used: one commercial cultivar (75I77RSF IPRO), planted by rural producers in the state of Acre, and two lineages from the Soybean Genetic Improvement Program of EMBRAPA Temperate Agriculture, PELBR15 -7016 and PELBR17-46, considered tolerant and sensitive to soil flooding, respectively.

Sowing was carried out in pots with a capacity of 8 L, containing substrate composed of a mixture of vegetable soil and washed sand, in the proportion of 1:1. With the aid of a scale, 1 kg of gravel was weighed and placed at the bottom of

the pots and then 8 kg of substrate was added. Before sowing, the seeds were inoculated with the commercial product Peat Inoculum Masterfix Soja at a dose of 100 g/50 kg of seeds, at a concentration of 5 x 10⁹ colony forming units of *Bradyrhizobium japonicum* and *B. elkanii* per gram. During the plant cycle, up to the V2 stage, second node, according to Ritchie, Hanway and Thompson (1982), pots were maintained at 70% of field capacity.

The field capacity for water treatments was previously established as the water content retained by the dry substrate after saturation and subsequent drainage of the excess. The mass of water retained in the substrate was considered as 100% of the field capacity. Based on this parameter, 70% FC was established for the irrigation of the pots. Irrigation maintenance was carried out by weighing the pots daily using a digital scale (ELGIN DP-15 Plus) and replacing the volume of transpired water.

The treatments consisted of control (without application of stress) and stressed, characterized by soil saturation, with application and maintenance of a water layer, approximately 3 cm above the soil surface, for a period of ten days and, subsequently, drainage of the water volume.

The application of the water layer was carried out in two moments of the plant. At the phenological stage V2, repeating in the same plots, and later for more ten days at the R2 stage, as described by Ritchie, Hanway and Thompson (1982). Other plots received substrate flooding only at the R2 stage, for ten days. In the control treatment, the plants were subjected to water availability conditions of 70% of field capacity throughout the plant cycle, with supplementary daily irrigation in case of water deficit.

During the plant cycle, three physiological evaluations were performed: measurement 1 – after flooding in the vegetative period (V2); measurement 2 – after flooding in the reproductive period (R2); and measurement 3 – ten days after draining the flood water (recovery).

Photosynthesis and gas exchange analyses were performed using an infrared gas analyzer – IRGA, model Li-6400XT (LI-COR Inc., CA, USA). Each measurement comprised net photosynthesis (A, in $\mu\text{mol m}^{-2} \text{s}^{-1}$), stomatal conductance (gs, in $\text{mol m}^{-2} \text{s}^{-1}$), leaf transpiration (E, in $\text{mmol m}^{-2} \text{s}^{-1}$) and the partial pressure of CO₂ (Ci, in Pa). The middle part of the leaflet was used for this purpose. In these measurements, the chamber temperature was maintained at 28 °C, the external CO₂ concentration (reference) was maintained at 400 ppm and the photosynthetically active photon flux density (PPFD) in the leaf was maintained at 1200 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$. The collected data was then used to obtain the water use efficiency (WUE), calculated from the ratio of A to E, and the efficiency of carboxylation (EC), calculated as the ratio of A to Ci.

At the same time as the gas exchange measurements, parameters related to chlorophyll a fluorescence were evaluated, using a fluorometer coupled to the IRGA, model Li-6400-40 (Li-Cor Inc., Lincoln, USA). The following parameters were assessed:

a) Actual quantum efficiency of the photosystem II:

$$([\Delta F/F_m' = (F_m' - F_s)/F_m']];$$

(b) Photochemical quenching:

$$[qP=(Fm'-Fs)/(Fm'-Fo')];$$

(c) Apparent rate of electron transport:

$$[ETR=((Fm'-Fs)/Fm')\times PPFD \times 0.5 \times 0.85];$$

(d) Potential quantum efficiency of photosystem II (after 30 minutes under dark conditions):

$$[Fv/Fm=(FmFo)/Fm];$$

(e) Non-photochemical quenching:

$$[NPQ=(Fm-Fm')/Fm'];$$

(f) Relative excess energy (EXC), calculated as:

$$EXC = [(Fv/Fm) - (\Delta F/Fm')]/(Fv/Fm).$$

For ETR evaluation, 0.5 was used as the fraction of excitation energy distributed to photosystem II in C3 plants and 0.85 as the fraction of light absorbed by leaves. Fm and Fo are, respectively, maximum and minimum fluorescence of dark-adapted leaves; Fm' and Fs are, respectively, maximum and dynamic equilibrium fluorescence in light-adapted leaves; and Fo' is the minimum fluorescence after far-red illumination of leaves previously exposed to light.

The data obtained were subjected to analysis of variance (ANOVA) and, when there was a significant difference at 5% probability level, Tukey test was performed to compare the means, with the aid of the statistical software Sisvar 5.0 (FERREIRA, 2011).

RESULTS AND DISCUSSION

The photosynthetic rate was affected by the water treatments applied, with significant interactions between the factors (Figure 1). Under soil flooding conditions in the vegetative period, at the V2 stage, net photosynthesis was reduced by 37% in the tolerant genotype, while no change was observed in the sensitive and local genotypes (Figure 1A). A similar behavior occurred with the treatments applied in the reproductive period, R2 stage, both for the plots that received stress in the vegetative/reproductive period and for those that were subjected to stress only in the reproductive period. The commercial genotype showed no reduction in the photosynthetic rate, while the others were strongly affected. The tolerant genotype had a reduction of 54% when subjected to soil flooding in the vegetative/reproductive stages and 50% in the reproductive stage; and the sensitive genotype was the one that showed the greatest reduction, 55% (V2/R2) and 70% (R2) compared to control plants (Figure 1B). In recovery, all genotypes showed a reduction in the photosynthetic rate, but the tolerant and sensitive ones had the lowest values (Figure 1C).

Stomatal conductance changed in the commercial genotype under water treatment in the vegetative stage (Figure

1D) and in the sensitive one in the reproductive period (Figure 1E). In the first stage of water treatment there was no interference in the activity of the stomata; however, when the stress was applied in the reproductive stage of soybean plants, it strongly affected them, with reductions of 51% and 21% in V2/R2 and R2, respectively, in the tolerant genotype, 63% (V2R2) and 71% (R2) in the sensitive genotype, and 32% (V2R2) and 38% (R2) in the local genotype (Figure 1E). As for the recovery evaluation, the plants showed behavior similar to that of the reproductive stage.

During the period of water stress, it is common for plants to adopt measures to face or tolerate the stress applied to them. Stomatal closure is a widely used mechanism to prevent or reduce stomatal conductance in leaves. In Figure 1, it is observed that the three soybean genotypes used in this study reduced stomatal opening when subjected to water stress in the reproductive stage (R2) and in recovery, altering gas exchange and consequently photosynthesis. Change in conductance is one of the first responses to stress. This occurs as a defense mechanism to reduce the loss of water by the leaves to the atmosphere, as the absorption of water by the roots becomes more difficult (SOUSA et al., 2016; RODRIGUEZ-DOMINGUEZ; BRODRIBB, 2020).

Related to the opening and closing of stomata, net photosynthesis was strongly affected by water stress in the tolerant and sensitive genotypes at both times of flooding (vegetative/reproductive and reproductive). Although the commercial genotype reduced stomatal conductance under soil flooding conditions, there was no reduction in photosynthetic rate (Figure 1E). Similar result was found by Garcia et al. (2020), who observed a reduction in the photosynthetic rate in soybean genotypes under flooding for two days. Alternatively, the decrease in photosynthesis values in plants subjected to soil waterlogging may be related to stomatal limitation caused by stomatal closure (TIAN et al., 2019).

Water treatments did not affect leaf transpiration of soybean genotypes in the vegetative stage (V2). As for the genotypes, only the commercial one showed a reduction (Figure 2A). After the stress in the reproductive period, the sensitive one showed less transpiration compared to the others, and when subjected to the soil flooding treatments, it had reductions in transpiration of 40% and 55% compared to the control, in the vegetative/reproductive and vegetative, respectively. In turn, the tolerant genotype showed changes in the V2/R2 stage (36%) and the commercial genotype remained indifferent to the stresses (Figure 2B). In recovery, the leaf transpiration behavior remained for the tolerant and sensitive genotypes, but the commercial one had a 20% reduction (Figure 2C).

An increase was observed in the internal concentration of CO₂ in the tolerant genotype under water stress in vegetative stage (Figure 2D), reproductive stage (Figure 2E) and also in recovery (Figure 2F), of 10%, 6% and 15% respectively. Sensitive and commercial genotypes did not show statistical differences for water treatments. In the flooding only in the reproductive stage and in the assessment of plant recovery, the commercial variety was the one that showed lower CO₂ concentration.

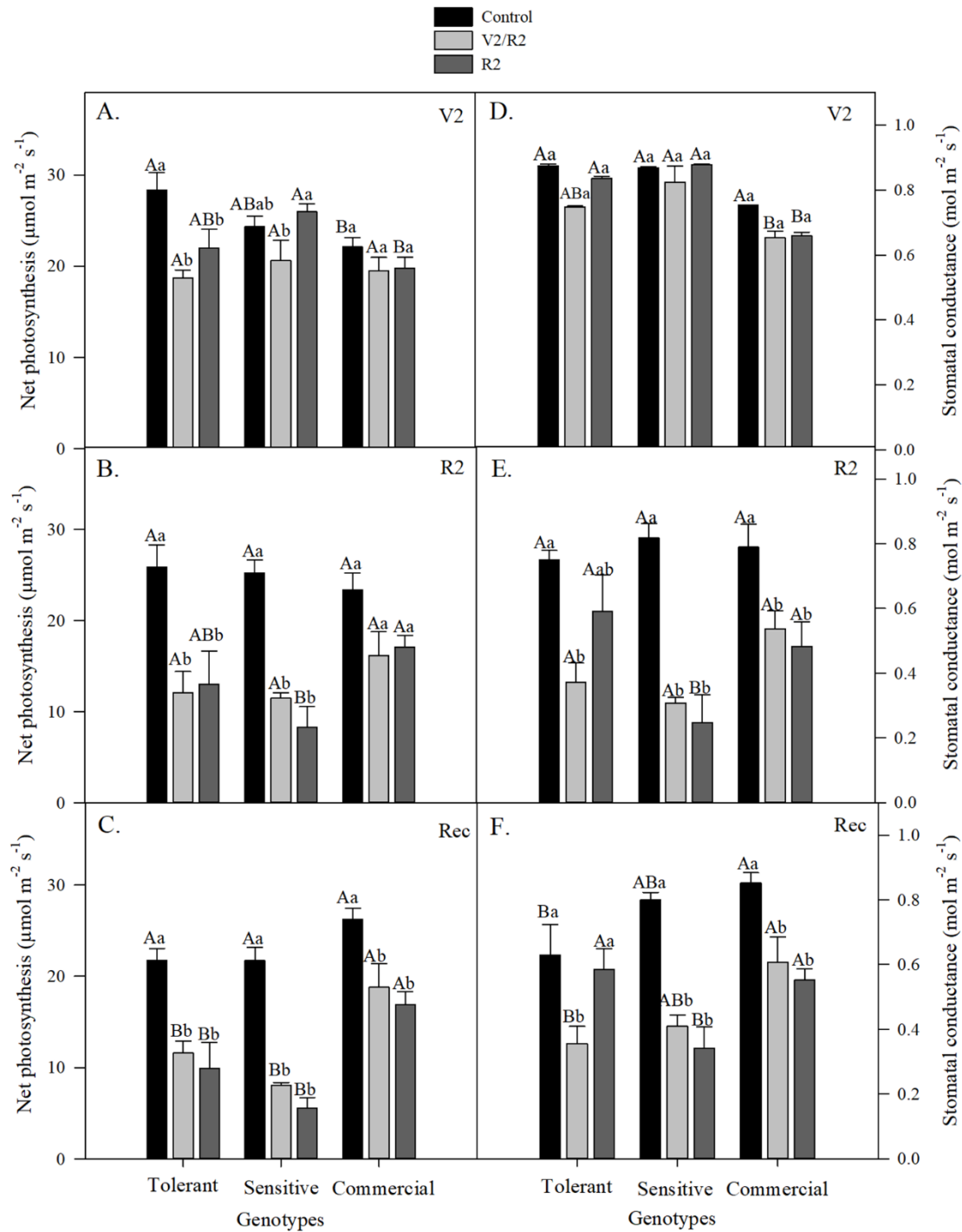


Figure 1. Net photosynthesis of three soybean genotypes at stages V2 (A), R2 (B) and recovery (C) and stomatal conductance at stages V2 (D), R2 (E) and recovery (F) under irrigated conditions, flooded by days in the vegetative and reproductive period or flooded in the reproductive period. Different capital letters indicate significant differences between genotypes for the same conditions and different lowercase letters indicate difference between water treatments for the same genotype, by the Tukey test ($p \leq 0.05$).

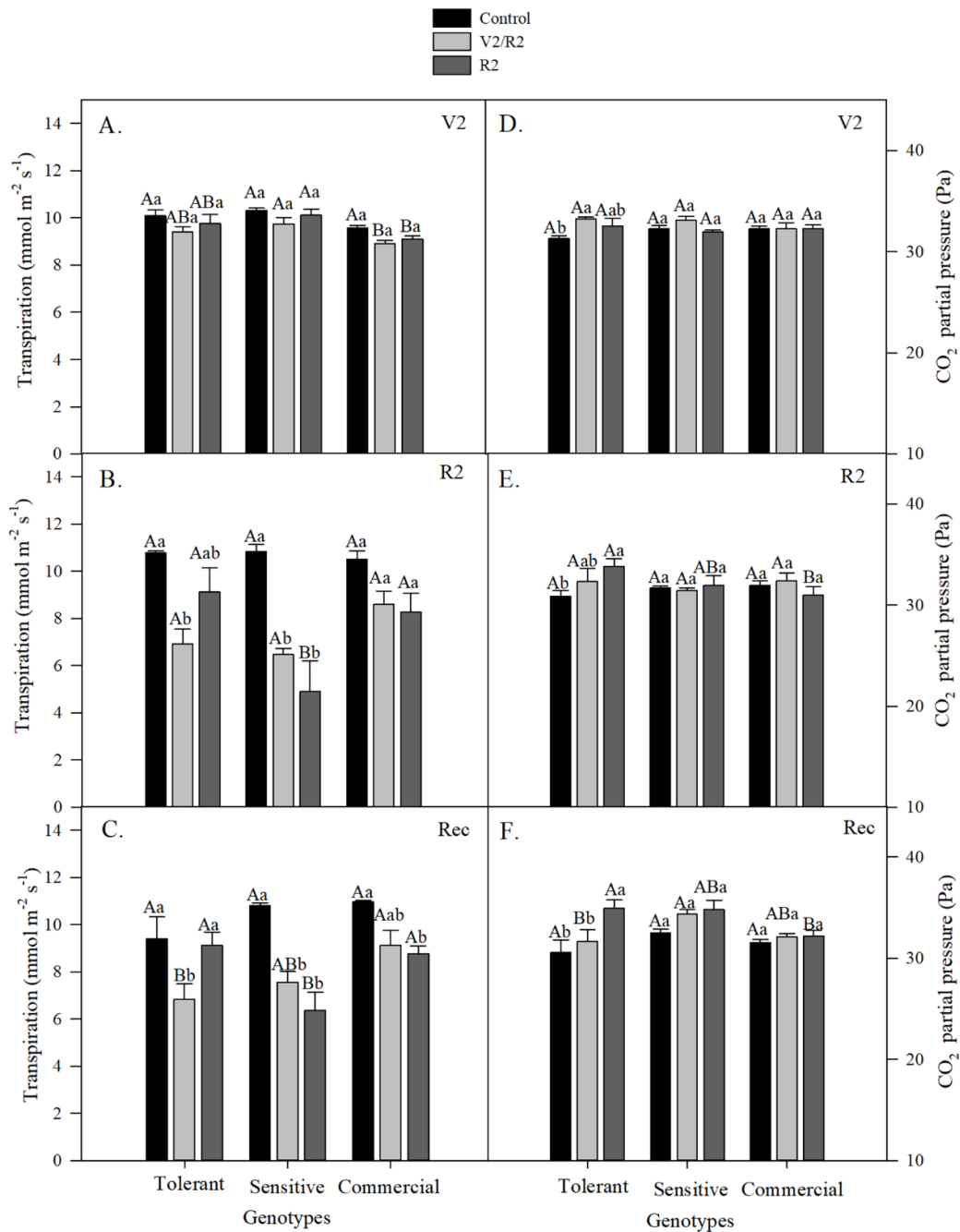


Figure 2. Leaf transpiration of three soybean genotypes at stages V2 (A), R2 (B) and recovery (C) and CO₂ partial pressure at stages V2 (D), R2 (E) and recovery (F) under irrigated conditions, flooded for days in the vegetative and reproductive period or flooded in the reproductive period. Different capital letters indicate significant differences between genotypes for the same conditions and different lowercase letters indicate difference between water treatments for the same genotype, by the Tukey test ($p \leq 0.05$).

Several adaptive responses are initiated by plants as a mechanism to alleviate the consequences of oxygen deficiency during flooding (KREUZWIESER; RENNENBERG, 2014). In particular, there are many metabolic changes that may confer tolerance on certain species to hypoxic conditions. However, the specific changes and the extent to which they occur may differ between the genotypes subjected to hypoxia, as shown in Figure 2, as the sensitive genotype reduced leaf transpiration in the water

treatment in the reproductive stage (Figure 2B) without affecting the internal concentration of CO₂ (Figure 2E), while the tolerant one had less leaf transpiration and increased the CO₂ concentration and the commercial one showed no difference between the treatments.

According to Borella et al. (2017), plants perform several morphological and physiological changes, in addition to biochemical ones, in response to flooding as a mechanism to reduce the metabolic need for energy and increase the

availability of oxygen to submerged tissues. All these adjustments underlie an important hypoxia survival strategy (ANTÓNIO et al., 2016). The mechanism carried out by the tolerant genotype of increasing the internal concentration of CO₂ under conditions of stress due to excess water in the soil reaffirms its adaptation to these environments. For instance, a high carbon demand is necessary to keep the metabolism operating under hypoxic conditions (BARICKMAN; SIMPSON; SAMS, 2019). Apparently, the increase in carbon flux arises to maintain glycolysis while the synthesis of storage products is negative (BORELLA et al., 2014). There was no statistical difference in water use efficiency and in the efficiency of carboxylation for the commercial genotype in

the two periods of soil flooding, V2/R2 and R2. The water treatment reduced water use efficiency in the tolerant soybean genotype by 39% under stress in the vegetative stage (Figure 3A) and by 43% under stress in the reproductive stage (Figure 3B). The genotypes from the genetic improvement program proved to be inefficient in recovering water use: the sensitive maintained reductions of 47% under stress in stages V2/R2 and 55% under stress in R2; and the tolerant showed recovery only in the vegetative/reproductive stage (Figure 3C). These same genotypes under soil flooding conditions were strongly affected in terms of carboxylation efficiency (Figure 3E) and remaining under these same conditions in the recovery evaluation (Figure 3F).

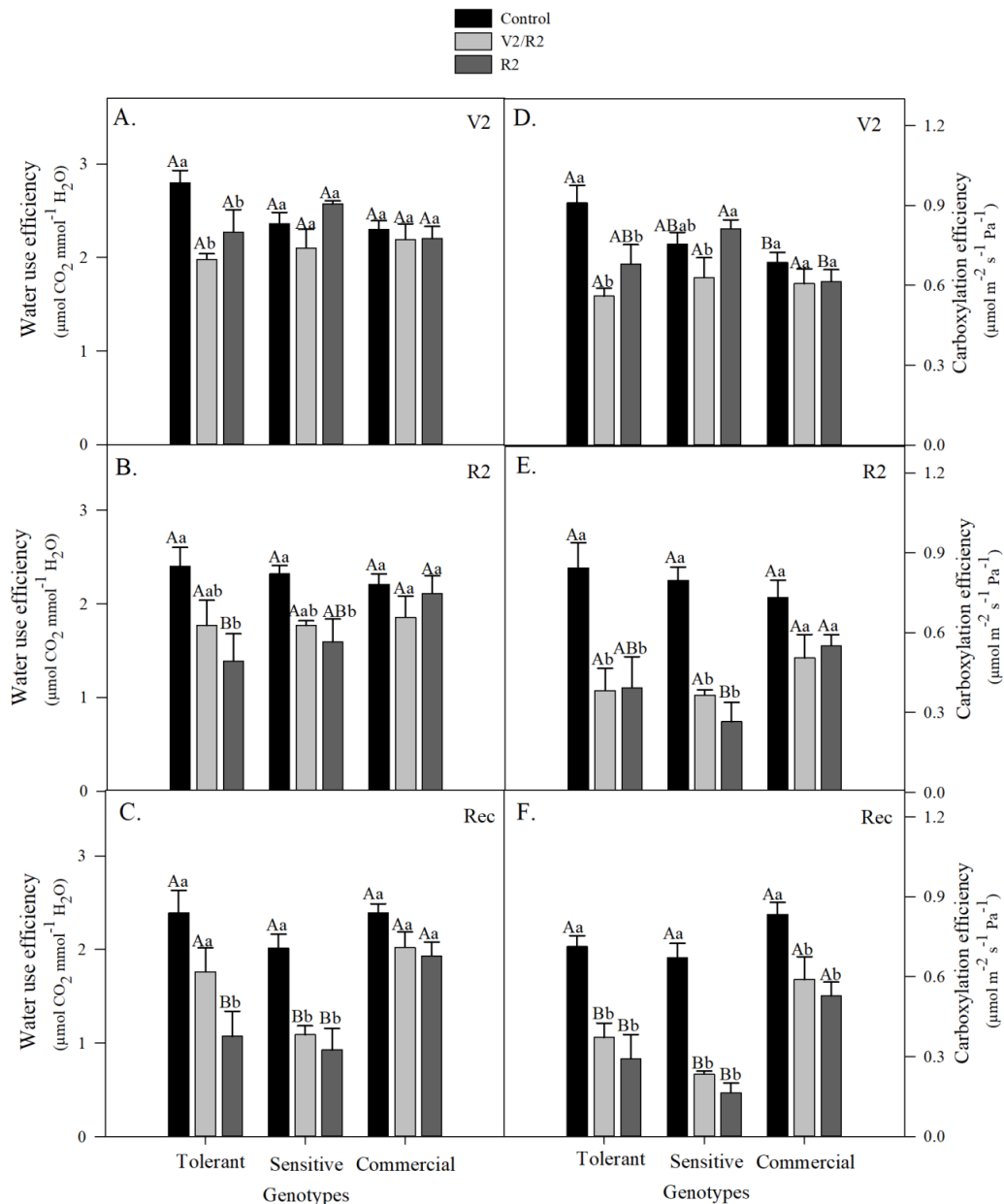


Figure 3. Water use efficiency (WUE) of three soybean genotypes at stages V2 (A), R2 (B) and recovery (C) and carboxylation efficiency at stages V2 (D), R2 (E) and recovery (F) under irrigated conditions, flooded for days in the vegetative and reproductive period or flooded in the reproductive period. Different capital letters indicate significant differences between genotypes for the same conditions and different lowercase letters indicate difference between water treatments for the same genotype, by the Tukey test ($p \leq 0.05$).

As a result of the water stress applied, the tolerant and sensitive genotypes had reduced water use efficiency in the two stages evaluated. The commercial genotype once again did not suffer from hypoxic conditions. Previous research has also indicated a decrease in WUE in cucumber plants subjected to waterlogging stress (BARICKMAN; SIMPSON; SAMS, 2019), and according to the authors this reduction can be explained by stomatal closure and reduced hydraulic conductivity of the roots or by negative regulation of the photosynthetic process and carbohydrate production, while increasing water loss through stomatal opening and transpiration. Just as the regulation of stomatal conductance is of paramount importance in controlling transpiration and also the entry of CO₂ inside the leaves, water use efficiency can also affect the availability of CO₂ to the carboxylation centers, thereby regulating the concentration of CO₂ inside the mesophyll, affecting the internal concentration of CO₂ and its access to carboxylation sites (BERTOLINO; CAINE; GRAY, 2019), which justifies that changes in water use efficiency reduced the efficiency of carboxylation in water treatments in the vegetative and reproductive stages, without recovery.

The greater efficiency of carboxylation observed in the commercial genotype indicates adaptation for survival in environments with periods of low oxygen availability, which is justified by the fact that the genotype is planted by producers in the state, unlike the results obtained by Honório et al. (2021) with araticum (*Annona crassiflora*), showing a decrease in carboxylation efficiency under conditions of water excess in the soil. Also, according to the authors, under flooding, damage evidenced by low values of chlorophyll a fluorescence may result in lower efficiency of carboxylation, as observed in the tolerant and sensitive genotypes.

The determination of chlorophyll a fluorescence signals is an important tool to assess the integrity of the photosynthetic apparatus and the possible influence of non-stomatal factors on carboxylation efficiency. Regarding chlorophyll a fluorescence, the results revealed a significant influence of soil flooding on the genotypes, sensitive and tolerant, at stage V2 (Figure 4A) and on all genotypes at V2/R2 (Figure 4B). No recovery of the genotypes was observed ten days after draining the water (Figure 4C); however, the variety planted by rural producers in the state was superior to the others in both periods of flooding (Figure 4C). The imposition of hypoxia in the vegetative stage of the plant caused a reduction in the actual quantum efficiency only in the tolerant and sensitive genotypes, of 37% and 20%, respectively (Figure 4A). For stress applied in the reproductive stage, all genotypes in the present study suffered from stress conditions and did not show recovery. As for the potential quantum efficiency of PSII, in the first flooding stage, vegetative, there was no effect on the genotypes (Figure 4D); however, in the second stage, reproductive, the tolerant genotype showed a difference only in the V2/R2 stage, while the sensitive genotypes showed differences in the vegetative/reproductive and in the reproductive periods (Figure 4E). Furthermore, the effects of hypoxic stress showed up later, as all genotypes failed to recover from water treatments (Figure

4F).

The reduction in the actual quantum efficiency, which measures the passage of electrons for photosynthesis, and in the potential quantum efficiency, which shows the integrity of the thylakoid membranes and proteins that form the photosystems, could have been the result of the limitation of the photosynthetic rate by hypoxic conditions to which the soybean genotypes were subjected. However, this modification was not enough to cause major problems in the photosystems, as shown by the small reduction in the potential quantum efficiency value of photosystem II (Figures 4D, 4E and 4F). According to Selmar and Kleinwächter (2013), the action of reducing the actual quantum efficiency and potential quantum efficiency, under flood conditions, is a photoprotection mechanism to minimize damage to the photosystem.

The values found for the potential quantum efficiency in the present work are within the expected range, as no treatment had averages below the proposed range. According to Silva et al. (2015), values of potential quantum efficiency ranging from 0.75 to 0.85 indicate that the photosynthetic apparatus is intact. Therefore, it can be inferred that the water stresses tested were not able to damage photosystem II.

There was no statistical difference between water treatments for non-photochemical quenching in the reproductive stage; on the other hand, the tolerant and sensitive genotypes showed lower values than those of the commercial genotype (Figure 5A). When soil flooding was applied in the reproductive stage, the sensitive genotype increased non-photochemical quenching by 57% in V2/R2 and 133% in R2 compared to the tolerant one. Furthermore, it also increased non-photochemical quenching by 118% and 147%, respectively, compared to the control (Figure 5B). At the time of recovery, the treatments did not differ (Figure 5C). Water stress in the vegetative stage affected, with a small loss, the electron transfer rate in the tolerant and sensitive genotypes (Figure 5D). In the reproductive stage, the loss was greater and occurred in all genotypes studied, with average reductions of 48% for the tolerant, 55% for the sensitive and 32% for the commercial (Figure 5E), with no recovery of the conditions in the plants (Figure 5F).

Non-photochemical quenching had a significant increase in the sensitive genotype under flooding conditions at stages V2/R2 and R2 (Figure 5B). This elevation is a mechanism of the plant to dissipate energy, when there is excess energy that is not being used photochemically, and is a resource widely used in plants under stress. In the recovery evaluation, the NPQ returned to standard values. However, all genotypes showed inhibition of the electron transfer rate under flooding in the reproductive stage and in recovery; however, it was more evident in the tolerant and sensitive genotypes. Carloto et al. (2020), when studying the development of *Eragrostis plana* and *Eragrostis pilosa* under soil flooding conditions, found that stress also resulted in a reduction in the electron transport rate, as well as lower growth and development of plants.

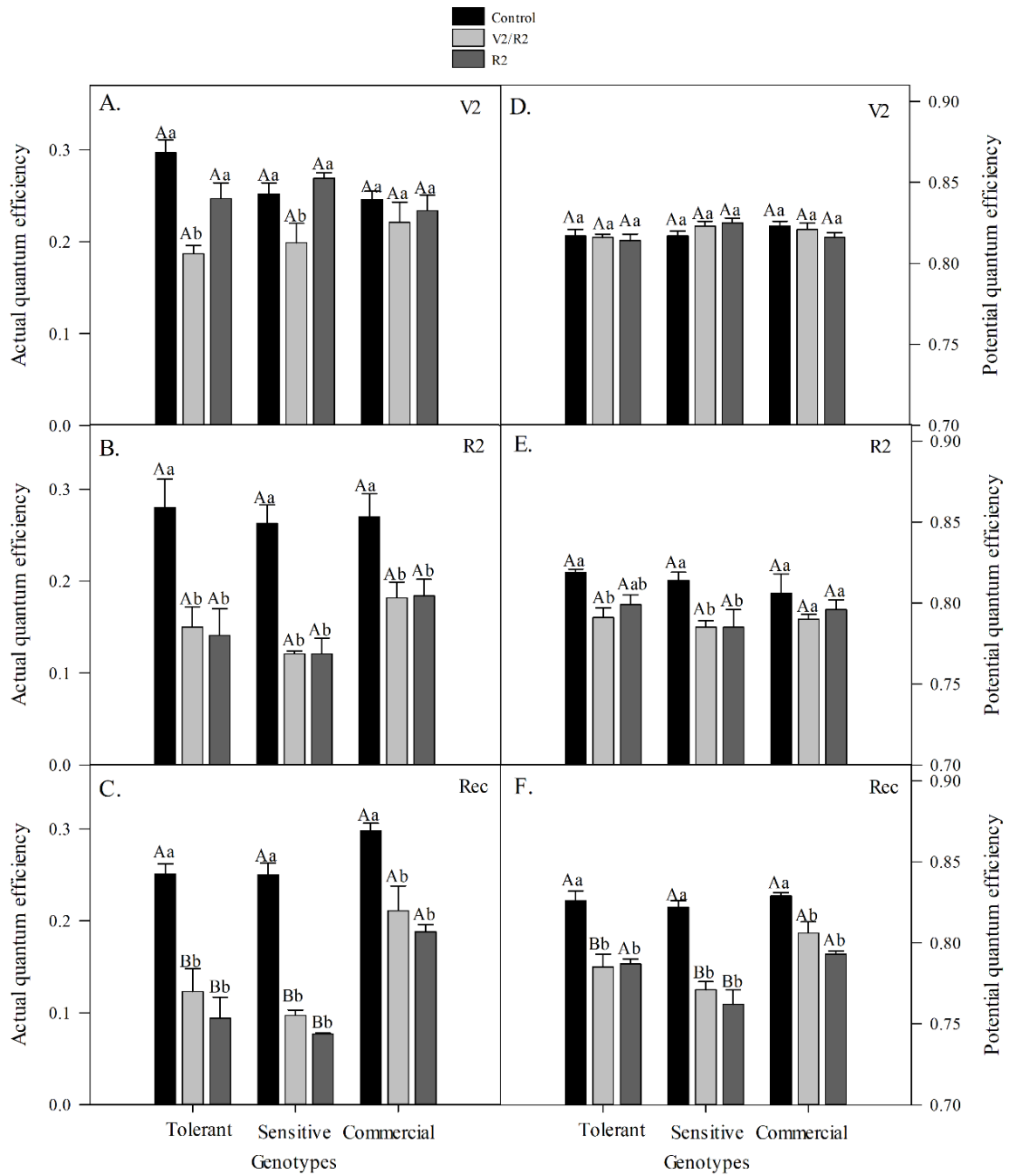


Figure 4. Actual quantum efficiency of three soybean genotypes at stages V2 (A), R2 (B) and recovery (C) and potential quantum efficiency at stages V2 (D), R2 (E) and recovery (F) under irrigated conditions, flooded for days in the vegetative and reproductive period or flooded in the reproductive period. Different capital letters indicate significant differences between genotypes for the same conditions and different lowercase letters indicate difference between water treatments for the same genotype, by the Tukey test ($p \leq 0.05$).

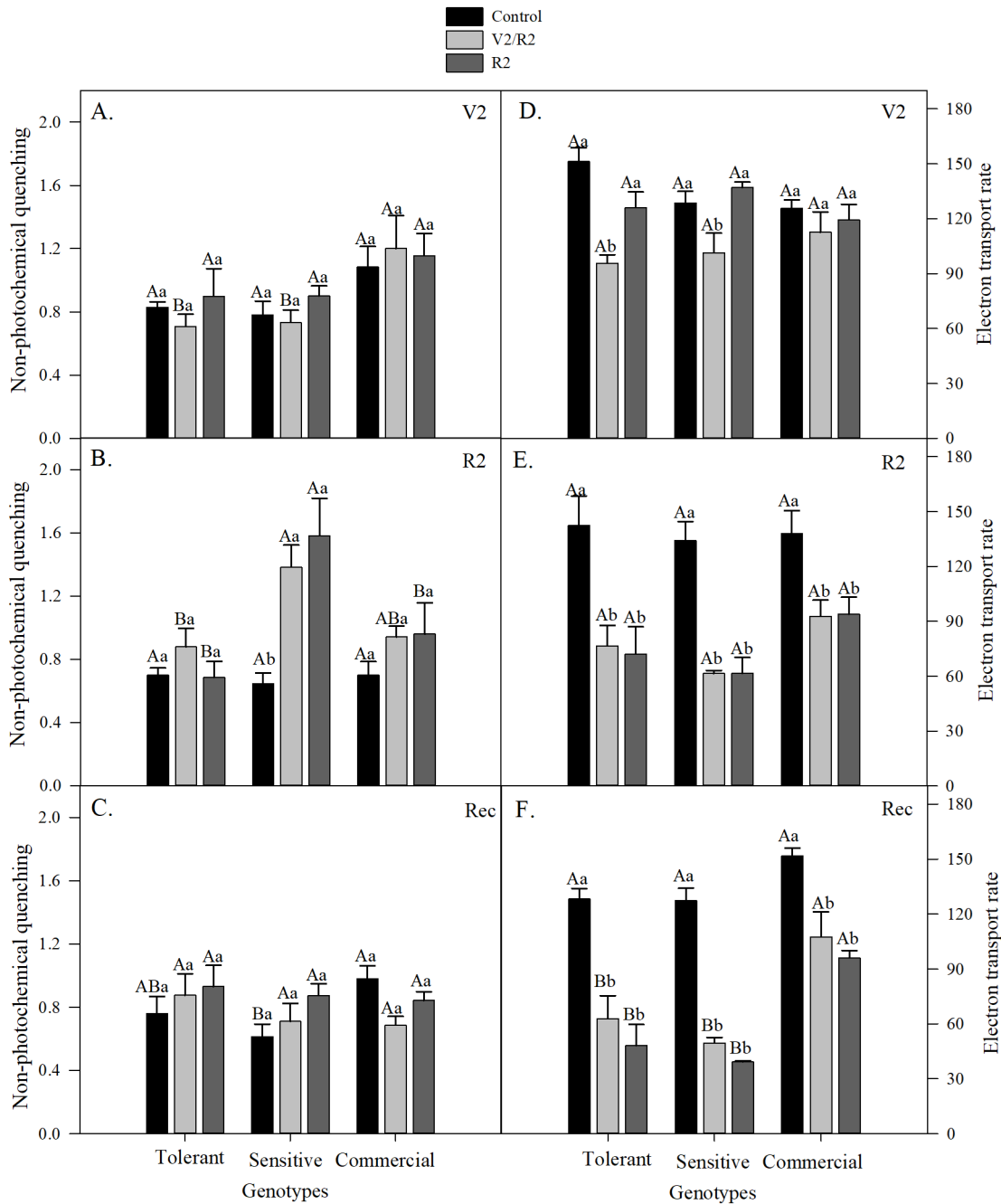


Figure 5. Non-photochemical quenching (NPQ) of three soybean genotypes at stages V2 (A), R2 (B) and recovery (C) and electron transport rate (ETR) at stages V2 (D), R2 (E) and recovery (F) under irrigated conditions, flooded for days in the vegetative and reproductive period or flooded in the reproductive period. Different capital letters indicate significant differences between genotypes for the same conditions and different lowercase letters indicate difference between water treatments for the same genotype, by the Tukey test ($p \leq 0.05$).

Soybean crop is generally intolerant to waterlogging stress (SATHI et al., 2022). Still according to the authors, under flood stress conditions, plants may show chlorosis, necrosis, defoliation, reduced growth, reduced nitrogen (N) fixation, yield loss and death in both the vegetative and reproductive stages. Therefore, the elucidation of physiological and biochemical changes resulting from exposure to soil flooding stress, in soybean genotypes, during different stages of crop development, is an important strategy

to overcome the negative effects of the environment on growth and productivity of the crop in areas where soil flooding occurs, common in the state of Acre. The development of strategies and methodologies for evaluating the genotypic response to hypoxic stress is shown to be an alternative with great potential to assist in the characterization and selection of genotypes with greater tolerance to flooding and consequent increase in production and productivity under this condition.

CONCLUSIONS

The commercial soybean cultivar planted by local rural producers proves to be more adapted to the conditions to which it was exposed in the two stages of the plant's life cycle, vegetative and reproductive stages, maintaining unaltered photosynthesis, stomatal conductance, leaf transpiration, water use efficiency, potential quantum efficiency and non-photochemical quenching. Also, the commercial genotype outperformed the tolerant one, which has a behavior similar to that of the sensitive one for most of the variables analyzed.

REFERENCES

- ANTÓNIO, C. et al. Regulation of primary metabolism in response to low oxygen availability as revealed by carbon and nitrogen isotope redistribution. **Plant Physiology**, 170: 43-56, 2016.
- ARGUS, R. E.; COLMER, T. D.; GRIERSON, P. F. Early physiological flood tolerance is followed by slow post-flooding root recovery in the dryland riparian tree *Eucalyptus camaldulensis* subsp. *refulgens*. **Plant, Cell & Environment**, 38: 1189-1199, 2015.
- 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**, 8: 1-15, 2019.
- BERTOLINO, L. T.; CAINE, R. S.; GRAY, J. E. Impact of stomatal density and morphology on water-use efficiency in a changing world. **Frontiers in Plant Science**. 2019, 10: 1-11, 2019.
- BORELLA, J. et al. Hypoxia-driven changes in glycolytic and tricarboxylic acid cycle metabolites of two nodulated soybean genotypes. **Environmental and Experimental Botany**, 133: 118-127, 2017.
- BORELLA, J. et al. Waterlogging-induced changes in fermentative metabolism in roots and nodules of soybean genotypes. **Scientia Agricola**, 71: 499-508, 2014.
- CARLOTO, B. W. et al. Response of *Eragrostis plana* and *Eragrostis pilosa* (L.) P. Beauv. submitted on flooded soil. **Acta Scientiarum Biological Sciences**, 42: 1-10, 2020.
- DANIEL, K.; HARTMAN, S. How plant roots respond to waterlogging. **Journal of Experimental Botany**, 75: 511-525, 2024.
- FERREIRA, D. F. Sisvar: a computer statistical analysis system. **Ciência e Agrotecnologia**, 35: 1039-1042, 2011.
- GARCIA, N. et al. Waterlogging tolerance of five soybean genotypes through different physiological and biochemical mechanisms. **Environmental and Experimental Botany**, 172: 1-8, 2020.
- HONÓRIO, A. B. M. et al. Impact of drought and flooding on alkaloid production in *Annona crassiflora* Mart. **Horticulturae**, 7: 1-14, 2021.
- KAUR, G. et al. Impacts and management strategies for crop production in waterlogged or flooded soils: a review. **Agronomy Journal**, 112, 1475-1501, 2020.
- KREUZWIESER, J.; RENNENBERG, H. Molecular and physiological responses of trees to waterlogging stress. **Plant Cell Environment**, 37: 2245-2259, 2014.
- LEÓN, J.; CASTILLO, M. C.; GAYUBAS, B. The hypoxia-reoxygenation stress in plants. **Journal of Experimental Botany**, 72: 5841-5856, 2020.
- LIAO, C. T.; LIN, C. H. Physiological adaptation of crop plants to flooding stress. **Proceedings National Science Council**, 25: 148-157, 2001.
- LORETI, E.; PERATA, P. The many facets of hypoxia in plants. **Plants**, 9: 1-14, 2020.
- MARCÍLIO, T. et al. Flooding and submersion-induced morphological and physiological adaptive strategies in *Lonchocarpus cultratus*. **Aquatic Botany**, 159: 1-10, 2019.
- MOURTZINIS, S.; CONLEY, S. P. Delineating soybean maturity groups across the United States. **Agronomy Journal**, 109: 1397-1403, 2017.
- NAKAMURA, M.; NOGUCHI, K. Tolerant mechanisms to O₂ deficiency under submergence conditions in plants. **Journal of Plant Research**, 133: 343-371, 2020.
- PIMENTEL, P. et al. Physiological and morphological responses of *Prunus* species with different degree of tolerance to long-term root hypoxia. **Scientia Horticulturae**, 180: 14-23, 2014.
- RITCHIE, S.; HANWAY, J. J.; THOMPSON, H. E. **How a soybean plant develops**. Ames: Yowa State University of Science and Technology, Cooperative Extension, 1982. 20 p. (Special Report, 53).
- RODRIGUEZ-DOMINGUEZ, C. M.; BRODRIBB, T. J. Declining root water transport drives stomatal closure in olive under moderate water stress. **New Phytologist**, 225: 126-134, 2020.
- SATHI, K. S. et al. Screening of soybean genotypes for waterlogging stress tolerance and understanding the physiological mechanisms. **Advances in Agriculture**, 2022: 1-14, 2022.
- SELMAR, D.; KLEINWÄCHTER, M. Influencing the product quality by deliberately applying drought stress during the cultivation of medicinal plants. **Industrial Crops and Productd**, 42: 558-566, 2013.
- SILVA, F. G. et al. Trocas gasosas e fluorescência da clorofila em plantas de berinjela sob lâminas de irrigação. **Revista Brasileira de Engenharia Agrícola e Ambiental**, 19: 946-952, 2015.

SOUSA, J. R. M. et al. Impacto das condições salinas e da adubação nitrogenada na produção de citros e nas trocas gasosas. **Revista Caatinga**, 29: 415-424, 2016.

TIAN, L. et al. Effects of waterlogging stress at different growth stages on the photosynthetic characteristics and grain yield of spring maize (*Zea mays* L.) Under field conditions. **Agricultural Water Management**, 218: 250-258, 2019.

WITTMANN, F. et al. Habitat specificity, endemism and the neotropical distribution of Amazonian white-water floodplain trees. **Ecography**, 36: 690-707, 2013.

ZAHRA, N. et al. Hypoxia and anoxia stress: Plant responses and tolerance mechanisms. **Journal of Agronomy and Crop Science**, 207: 249-84, 2021.

ZHOU, W. et al. Plant waterlogging/flooding stress responses: From seed germination to maturation. **Plant Physiology and Biochemistry**, 148: 228-236, 2020.

ZHOU, J. et al. Qualification of soybean responses to flooding stress using UAV-based imagery and deep learning. **Plant Phenomics**, 2021: 1-13, 2021.