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Growth, development, and photosynthetic performance of two soybean lineages in response to drought

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ABSTRACT: Drought stress is a common environmental factor that constrains plants from expressing their ecophysiological potential, disrupting various physiological and biochemical processes. Hence, the objective of this work was to evaluate the growth, development and photosynthetic performance under drought in the vegetative phenological stage of soybean in two lineages with potential difference tolerance to this abiotic stress, lineages ('Vx-08-10819' and 'Vx-08-11614'. For this purpose, biometric traits of development, relative water content in leaves, photosynthetic pigments, gas exchange, and chlorophyll *a* fluorescence were evaluated. The experimental design was a randomized block design with 4 replications and arranged in a 2 × 3 factorial scheme, comprising of two soybean lineages (Vx-08-10819 and Vx-08-11614) in combination with three water availability [100% (control), 60%, and 40% of field capacity]. Relative water content in leaves, total leaf area, and shoot dry weight of lineage Vx-08-10819 were not changed after exposure to drought. Besides that, photosynthetic capacity of lineage Vx-08-10819 was less affected than lineage Vx-08-11614 to drought, showing that this lineage is tolerant to this abiotic stress in at vegetative stage V4.
Keywords: chlorophylls; gas exchange; *Glycine max* (L.) Merr; water relations.

Crescimento, desenvolvimento e desempenho fotossintético de duas linhagens de soja em resposta à seca

RESUMO: O estresse hídrico é um fator ambiental comum que impede as plantas de expressarem seu potencial ecofisiológico, interrompendo vários processos fisiológicos e bioquímicos. Portanto, o objetivo deste trabalho foi avaliar o crescimento, o desenvolvimento e o desempenho fotossintético sob seca na fase fenológica vegetativa da soja em duas linhagens com potencial diferença na tolerância a este estresse abiótico, as linhagens Vx-08-10819 e Vx-08-11614. Para tanto, foram avaliadas características biométricas de desenvolvimento, teor relativo de água nas folhas, pigmentos fotossintéticos, trocas gasosas e fluorescência da clorofila *a*. O delineamento experimental foi em blocos casualizados com 4 repetições e dispostos em esquema fatorial 2 × 3, composto por duas linhagens de soja (Vx-08-10819 e Vx-08-11614) em combinação com três disponibilidades hídricas [100% (controle), 60% e 40% da capacidade de campo]. O conteúdo relativo de água nas folhas, a área foliar total e o peso seco da parte aérea da linhagem Vx-08-10819 não foram alterados após a exposição à seca. Além disso, a capacidade fotossintética da linhagem Vx-08-10819 foi menos afetada do que a linhagem Vx-08-11614 à seca, mostrando que esta linhagem é tolerante à este estresse abiótico no estágio vegetativo V4.
Palavras-chave: clorofilas; troca gasosa; *Glycine max* (L.) Merr; relações hídricas.

1. INTRODUCTION

Soybean (*Glycine max* (L.) Merrill) is grown worldwide, with several industrial applications and great importance in human and animal nutrition, as an important source of protein meal and vegetable oil (VOLLMANN et al., 2000; BEZERRA et al., 2015). Soybean provides more than half of the world's vegetable oil and two-thirds of its protein meal (LAPAZ et al., 2020).

Currently, several Brazilian soybean producing regions suffer from drought, mainly in sandy soils and under high air temperatures, where the risk of yield losses due to water and nutrient deficits is higher (FRANCHINI et al., 2017). This situation could become worse with climate change. According to Hlaváčová et al. (2018), an increase in the occurrence of extreme weather events is expected, such as short periods of high temperatures and periods of drought, with negative impacts on agricultural production.

Drought stress is a common environmental factor that constrains plants from expressing their ecophysiological potential (KRON et al., 2008; HAGHIGHI et al., 2020), disrupting various physiological and biochemical processes, such as membrane integrity, pigment content, osmotic adjustments, water relations, primary metabolism, stomatal closure, and photosynthetic activity (HLAVÁČOVÁ et al., 2018; TANKARI et al., 2021), which can limit yield (SINGH; REDDY, 2011).

Depending on lineages traits, soybeans need about 450 to 700 mm of water during cultivation (MANAVALAN et al., 2009), reaching maximum demand at the reproductive stage that is the most drought sensitive (ROSA et al., 2020). However, the drought during the early vegetative stage can influence pod development by the delay of node development (KIM et al., 2021), since soybean plants under drought commonly show reduced net photosynthesis due to the decrease in stomatal conductance (MESQUITA et al., 2020), resulting in a reduction in the intercellular CO_2 concentration, and also affecting electron transport and photophosphorylation (CATUCHI et al., 2011; MESQUITA et al., 2020).

In this way, the objective of this work was to evaluate the growth, development and photosynthetic performance under drought in the vegetative phenological stage V4 (Fehr; Caviness, 1971) of soybean in two lineages with potential difference tolerance to this abiotic stress, lineages 'Vx-08-10819' and 'Vx-08-11614', tolerant and sensitive to drought, respectively (ROSA et al., 2020). For this purpose, biometric traits of development, relative water content in leaves, photosynthetic pigments, gas exchange, and chlorophyll *a* fluorescence were evaluated.

2. MATERIAL AND METHODS

2.1. Plant growth conditions

Seeds of soybean lineages Vx-08-10819 and Vx-08-11614 were obtained from the Soybean Breeding Program for Quality Traits of the Agricultural Biotechnology Research Institute (Bioagro) at the Federal University of Viçosa, Brazil.

The experiments were conducted in a greenhouse covered with transparent polyethylene and protected on the sides with 50% shading. During the experiment, the average temperature and humidity of the greenhouse were 27°C and 67%, respectively. Seeds of the Vx-08-10819 and Vx-08-11614 lineages were germinated in a Bioplant substrate (Bioplant Agrícola Ltda., Nova Ponte, MG, Brazil). Four seedlings were grown per 9-kg pot in a mixture of soil and sand, in the ratio 2:1. Fertilization was carried out with 10 g of the formulation 4-14-8 (N-P-K). All pots were weighed and hydrated to maintain field capacity at 100%. When the plants reached the V4 growth stage, the irrigation was interrupted, except in the control. Then, for three days, the weight of the pots was monitored daily to maintain 60 and 40% field capacity. The control was maintained at 100% field capacity.

2.2. Relative water content and crop development

Leaf discs (6 mm diameter) were collected from fully expanded leaves, weighed, and placed in water for saturation to analyse the relative water content (RWC), which was obtained by the formula: Leaf RWC (%) = ((FW-DW)/(TW-DW)) × 100, where FW is fresh weight, DW is dry weight, and TW is turgid weight. The hydrated discs were then weighed again and dried to determine dry weight (Turner 1981). Subsequently, total leaf area (LA) and specific total leaf area (SLA) were evaluated using the LI-3100C area meter (LI-COR Biosciences, Lincoln, NE, USA). The shoot height (SH) was evaluated with the aid of a ruler. Lastly, the shoot was oven dried at 65 °C for 72 h and the shoot dry weight (SDW) was determined.

2.3. Photosynthetic pigments

Leaf discs (6 mm diameter) from fully expanded leaves were immersed in dimethyl sulfoxide saturated with calcium carbonate. Then, the absorbance of the samples was evaluated at 665.1, 649.1, and 480 nm to calculate the content of chlorophyll *a* (Chl *a*), *b* (Chl *b*), and of total chlorophyll (Total Chl) and carotenoids (CAR) (WELLBURN, 1994).

2.4. Gas exchange and chlorophyll *a* fluorescence

Gas exchange traits were determined on fully-expanded leaves at the same time that chlorophyll *a* fluorescence was measured using an open-flow infrared gas exchange analyzer system equipped with the LI-6400-40 leaf chamber fluorometer (LI-COR Biosciences, Lincoln, NE, USA). The net CO_2 assimilation rate (A), stomatal conductance (gs), internal CO_2 concentration (Ci), and transpiration rate (E) were measured from 8:00 to 10:00 a.m. (solar time), when A was at its maximum, under artificial photosynthetically active radiation (i.e., 1,000 μmol photons m^{-2} s^{-1} at the leaf level and 400 μmol CO_2 mol^{-1} air), at 25°C, with vapor pressure deficit maintained at ≈1.0 kPa and amount of blue light set to 10% of the photosynthetic photon flux density to optimize stomatal aperture. Intrinsic water use efficiency ($_{int}$WUE) was calculated as A/gs ratio.

The slow phase of chlorophyll *a* fluorescence induction, fluorescence of a light-adapted sample measured briefly before the application of a saturation pulse (F), and maximum fluorescence of a light-adapted sample (Fm') were obtained sequentially by applying a saturation pulse of actinic light (>3,000 μmol photons m^{-2} s^{-1}). The minimal fluorescence traits of the illuminated plant tissue (F0') and the fraction of open PSII centres (qP) were calculated from F and Fm'. The effective quantum yield of photosystem II photochemistry (ΦPSII) was used to estimate the apparent electron transport rate (ETR). The photochemical quenching coefficient was calculated as qP = (Fm' - Fs)/(Fm' - F0') and the quantum efficiency of open PSII reaction centres (Fv' / Fm') was calculated as (Fm'- Fo')/Fm'.

2.5. Experimental design and statistical analysis

The experimental design was a randomized block design with 4 replications and arranged in a 2 × 3 factorial scheme, comprising of two soybean lineages (Vx-08-10819 and Vx-08-11614) in combination with three water availability [100% (control), 60%, and 40% of field capacity].

Normality and homoscedasticity of the data were analyzed using the Shapiro-Wilk and Bartlett tests, respectively, both at 0.05 probability. Then, the data were subjected to analysis of variance (ANOVA) using the F test ($p \leq 0.05$). When significant, the traits were subjected to the Scott-Knott test ($p < 0.05$). As supplementary analysis, principal component analysis (PCA) was performed using 'FactoMineR,' 'factoextra,' and 'ggplot2' packages. All statistical analysis of the data was performed using protocols developed in the R software (R DEVELOPMENT CORE TEAM, 2019).

3. RESULTS

3.1. Relative water content and crop development

The relative water content in the leaves of lineage Vx-08-11614 was reduced after exposure to both drought conditions, which resulted in lower values when compared to the plants of lineage Vx-08-10819 (Figure 1). Conversely, in

Vx-08-10819, there were no differences in RWC between the different water availabilities (Figure 1).

The values of LA, SDW and SH decreased in line Vx-08-11614 after exposure to both drought conditions, with greater reductions observed after 40% of field capacity (Figure 2A, 2C–D). After to drought, Vx-08-10819 reduced SLA (40% of field capacity) and SH (60% and 40% of field capacity) (Figure 2B, 2D).

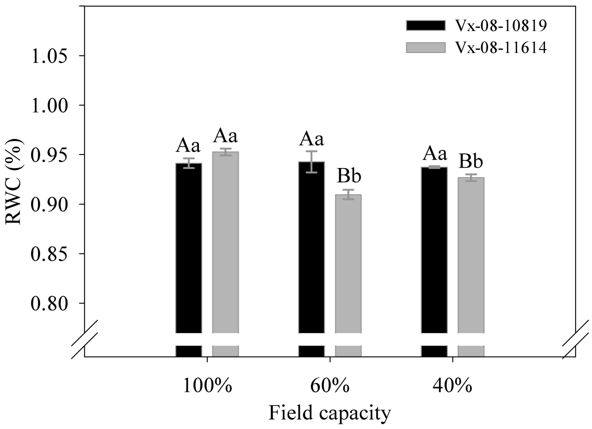

Figure 1. Relative water content in leaves – RWC in leaves of two soybean lineages, 'Vx-08-10819' and 'Vx-08-11614', during vegetative stage V4 after exposure to different water availability: 100% (control), 60%, and 40% of field capacity. Different letters indicate significant differences according to the Scott-Knott test (p < 0.05). Uppercase letters compare the different soybean lineages in the same water availability, while lowercase letters compare each soybean lineage between different water availability. Vertical bars represent the standard error.

Figura 1. Conteúdo relativo de água – RWC nas folhas em folhas de duas linhagens de soja, Vx-08-10819 e Vx-08-11614, durante o estágio vegetativo V4 após exposição a diferentes disponibilidades hídricas: 100% (controle), 60% e 40% da capacidade de campo. Letras diferentes indicam diferenças significativas de acordo com o teste de Scott-Knott (p < 0,05). Letras maiúsculas comparam as diferentes linhagens de soja na mesma disponibilidade hídrica, enquanto letras minúsculas comparam cada linhagem de soja entre diferentes disponibilidades hídricas. As barras verticais representam o erro padrão.

3.2. Photosynthetic performance

Reductions in Chl *a* and Total Chl content were observed in Vx-08-11614 after exposure to 60% of field capacity (Figure 3A, 3C). Conversely, Chl *b* content was not modified after exposure to both drought conditions (Figure 3B). Between the two soybean lineages, Vx-08-10819 had the highest Chl *a* content (60% of field capacity) and the highest Total Chl content (60% and 40% of field capacity), while Vx-08-11614 showed higher Chl *a* content after exposure to 40% of field capacity (Figure 3A, 3C). Regarding CAR content, there was an increase in Vx-08-10819 after exposure to 40% of field capacity (Figure 3D). Among the tested lineages, Vx-08-10819 showed higher CAR values in both drought conditions.

After water restriction, both lineages had a decreased *A*, but it remained higher in Vx-08-10819 (Figure 4A). The values of gs, *E* and Ci were reduced in both lineages after exposure to both drought conditions, with greater reductions in Vx-08-11614 (Figure 4B–D). Intrinsic water use efficiency increased similarly in both lineages after exposure to water restriction (Figure 4E).

In Vx-08-10819, there were no differences in ΦPSII, ETR, qP, and Fv'/Fm' between the different water availabilities (Figure 5A–D). In contrast, Vx-08-11614 showed the opposite response, reducing these traits after water restriction. Thus, among the lineages, Vx-08-11614 presented the lowest values for these traits in both drought conditions (Figure 5A–D).

3.3. PCA analysis

The first two principal components explained 63.3% of the total variation among traits. Soybean lineages were separated into two groups by their responsiveness to both drought conditions. The Vx-08-10819 was strongly linked to a range of photosynthetic traits, RCW, and SH (Figure 6).

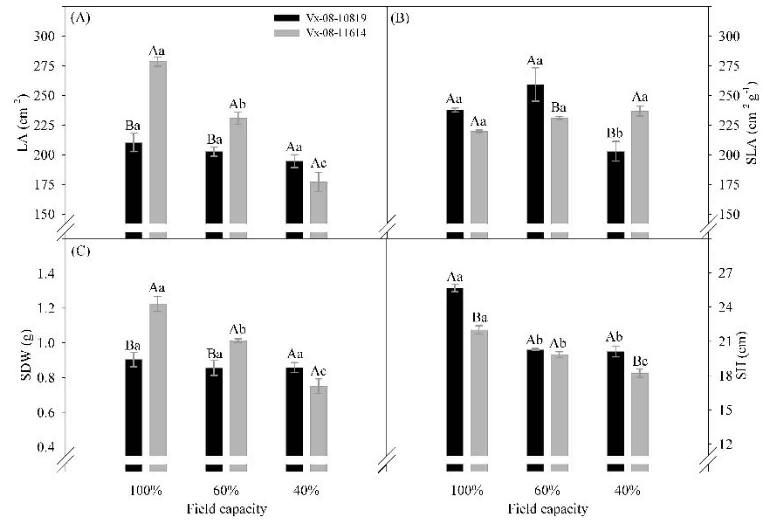

Figure 2. Total leaf area – LA (A), specific total leaf area – SLA (B), shoot dry weight – SDW (C), and shoot height – SH (D) of two soybean lineages, 'Vx-08-10819' and 'Vx-08-11614', during vegetative stage V4 after exposure to different water availability: 100% (control), 60%, and 40% of field capacity. Different letters indicate significant differences according to the Scott-Knott test (p < 0.05). Uppercase letters compare the different soybean lineages in the same water availability, while lowercase letters compare each soybean lineage between different water availability. Vertical bars represent the standard error.

Figura 2. Área foliar total – LA (A), área foliar específica total – SLA (B), massa seca da parte aérea – SDW (C) e altura da parte aérea – SH (D) de duas linhagens de soja, Vx-08-10819 e Vx-08-11614, durante o estágio vegetativo V4 após exposição a diferentes disponibilidades hídricas: 100% (controle), 60% e 40% da capacidade de campo. Letras diferentes indicam diferenças significativas de acordo com o teste de Scott-Knott (p < 0,05). Letras maiúsculas comparam as diferentes linhagens de soja na mesma disponibilidade hídrica, enquanto letras minúsculas comparam cada linhagem de soja entre diferentes disponibilidades hídricas. As barras verticais representam o erro padrão.

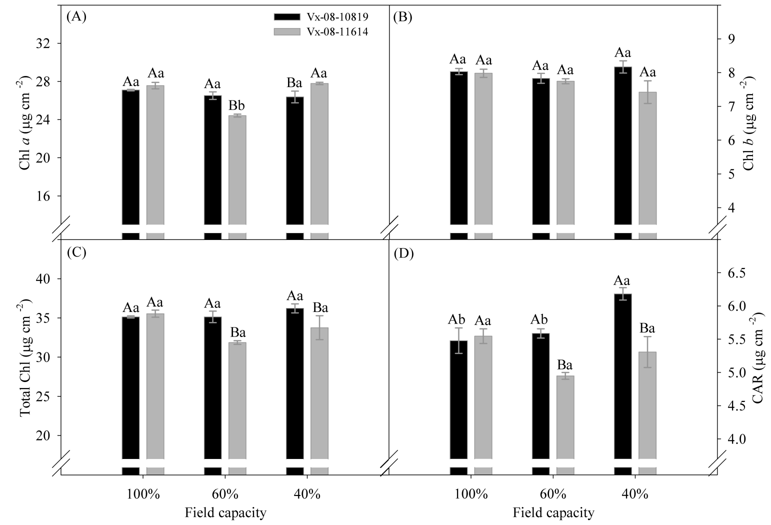

Figure 3. Chlorophyll *a* – Chl *a* (A), chlorophyll *b* – Chl *b* (B), total chlorophyll – Total Chl (C), and carotenoids – CAR (D) contents of two soybean lineages, 'Vx-08-10819' and 'Vx-08-11614', during vegetative stage V4 after exposure to different water availability: 100% (control), 60%, and 40% of field capacity. Different letters indicate significant differences according to the Scott-Knott test ($p < 0.05$). Uppercase letters compare the different soybean lineages in the same water availability, while lowercase letters compare each soybean lineage between different water availability. Vertical bars represent the standard error.

Figura 3. Conteúdo de clorofila a – Chl a (A), clorofila b – Chl b (B), clorofila total – Chl total (C) e carotenóides – CAR (D) de duas linhagens de soja, Vx-08-10819 e Vx-08-11614, durante o estágio vegetativo V4 após exposição a diferentes disponibilidades hídricas: 100% (controle), 60% e 40% da capacidade de campo. Letras diferentes indicam diferenças significativas de acordo com o teste de Scott-Knott ($p < 0,05$). Letras maiúsculas comparam as diferentes linhagens de soja na mesma disponibilidade hídrica, enquanto letras minúsculas comparam cada linhagem de soja entre diferentes disponibilidades hídricas. As barras verticais representam o erro padrão.

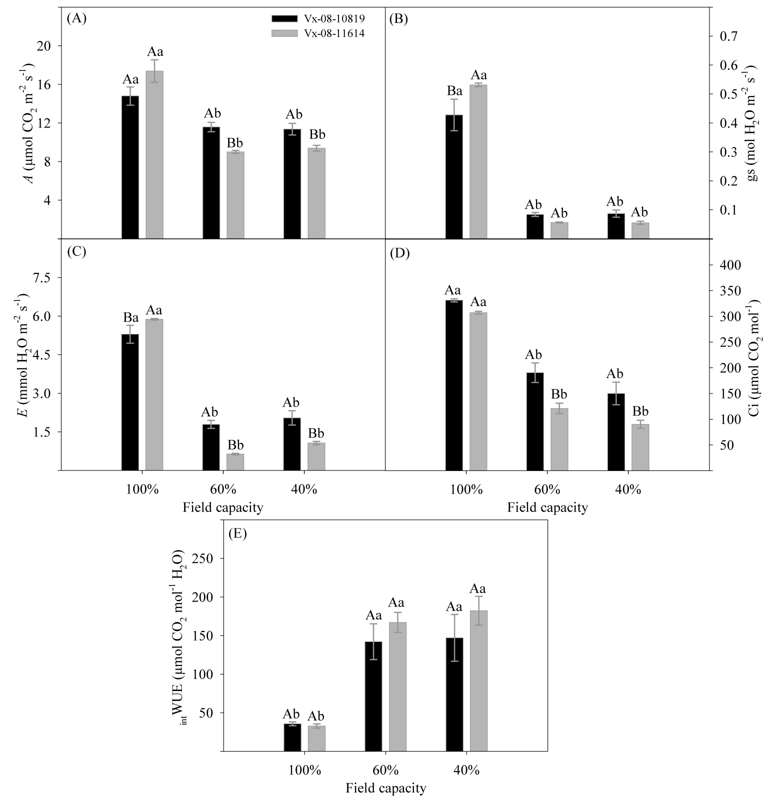

Figure 4. Net CO_2 assimilation rate – A (A), stomatal conductance – gs (B), transpiration rate – E (C), internal CO_2 concentration – Ci (D), and intrinsic water use efficiency – $_{int}$WUE (E) of two soybean lineages, 'Vx-08-10819' and 'Vx-08-11614', during vegetative stage V4 after exposure to different water availability: 100% (control), 60%, and 40% of field capacity. Different letters indicate significant differences according to the Scott-Knott test ($p < 0.05$). Uppercase letters compare the different soybean lineages in the same water availability, while lowercase letters compare each soybean lineage between different water availability. Vertical bars represent the standard error.

Figura 4. Taxa de assimilação líquida de CO_2 - A (A), condutância estomática - gs (B), taxa de transpiração - E (C), concentração interna de CO_2 - Ci (D) e eficiência intrínseca do uso da água - $_{int}$WUE (E) de duas linhagens de soja, Vx-08-10819 e Vx-08-11614, durante o estágio vegetativo V4 após exposição a diferentes disponibilidades hídricas: 100% (controle), 60% e 40% da capacidade de campo. Letras diferentes indicam diferenças significativas de acordo com o teste de Scott-Knott ($p < 0,05$). Letras maiúsculas comparam as diferentes linhagens de soja na mesma disponibilidade hídrica, enquanto letras minúsculas comparam cada linhagem de soja entre diferentes disponibilidades hídricas. As barras verticais representam o erro padrão.

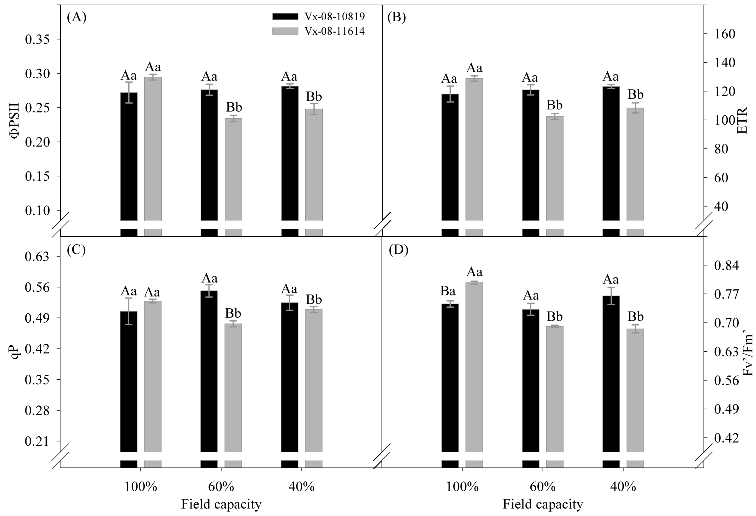

Figure 5. Effective quantum yield of PSII – ΦPSII (A), electron transport rate – ETR (B), photochemical quenching coefficient – qP (C), and quantum efficiency of open PSII reaction centres – Fv' / Fm' (D) of two soybean lineages, 'Vx-08-10819' and 'Vx-08-11614', during vegetative stage V4 after exposure to different water availability: 100% (control), 60%, and 40% of field capacity. Different letters indicate significant differences according to the Scott-Knott test ($p < 0.05$). Uppercase letters compare the different soybean lineages in the same water availability, while lowercase letters compare each soybean lineage between different water availability. Vertical bars represent the standard error.

Figura 5. Rendimento quântico efetivo do PSII – ΦPSII (A), taxa de transporte de elétrons – ETR (B), coeficiente de extinção fotoquímica – qP (C) e eficiência quântica de centros abertos de reação PSII – Fv' / Fm' (D) de duas linhagens de soja, Vx-08-10819 e Vx-08-11614, durante o estágio vegetativo V4 após exposição a diferentes disponibilidades hídricas: 100% (controle), 60% e 40% da capacidade de campo. Letras diferentes indicam diferenças significativas de acordo com o teste de Scott-Knott ($p < 0,05$). Letras maiúsculas comparam as diferentes linhagens de soja na mesma disponibilidade hídrica, enquanto letras minúsculas comparam cada linhagem de soja entre diferentes disponibilidades hídricas. As barras verticais representam o erro padrão.

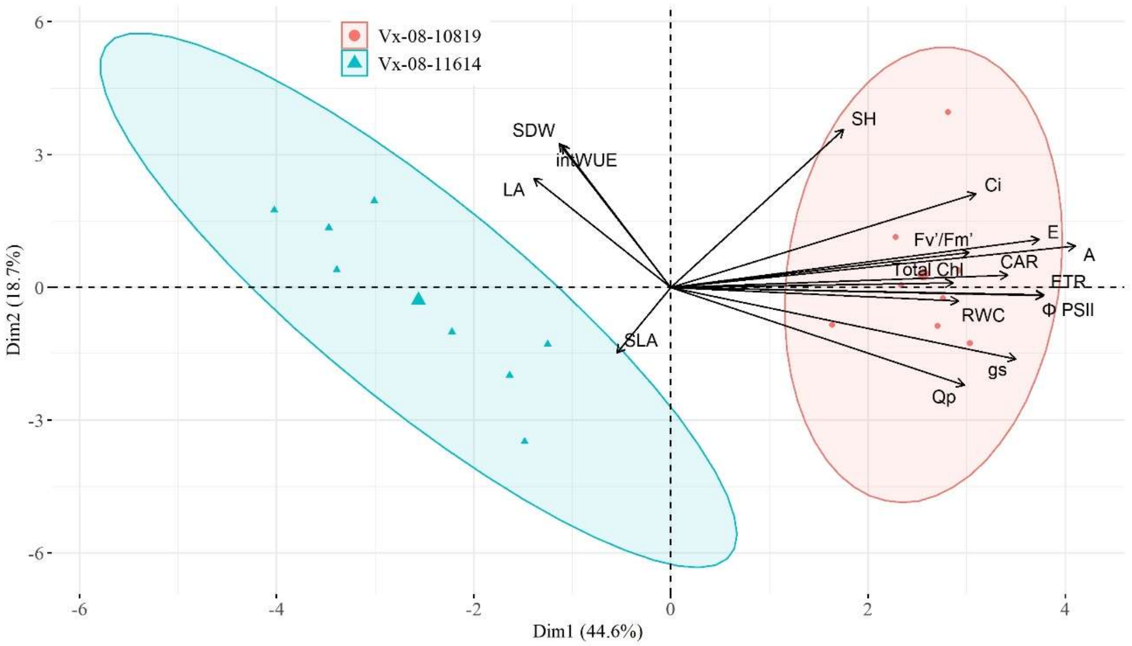

Figure 6. Biplot component analysis of the relative water content in leaves, crop development, and photosynthetic performance of two soybean lineages, 'Vx-08-10819' and 'Vx-08-11614', under 60% and 40% of field capacity. Relative water content in leaves – RWC, total leaf area – LA, specific total leaf area – SLA, shoot dry weight – SDW, and shoot height – SH, total chlorophyll – Total Chl, carotenoids – CAR, net CO_2 assimilation rate – *A*, stomatal conductance – gs, transpiration rate – *E*, internal CO_2 concentration – Ci, intrinsic water use efficiency – $_{int}$WUE, effective quantum yield of photosystem II – ΦPSII, electron transport rate – ETR, photochemical quenching coefficient – qP, and quantum efficiency of open PSII reaction centres – Fv' / Fm'.

Figura 6. Análise de componentes biplot do conteúdo relativo de água nas folhas, desenvolvimento da cultura e desempenho fotossintético de duas linhagens de soja, Vx-08-10819 e Vx-08-11614, sob 60% e 40% da capacidade de campo. Conteúdo relativo de água nas folhas – RWC, área foliar total – LA, área foliar específica total – SLA, massa seca da parte aérea – SDW, altura da parte aérea – SH, clorofila total – Chl total, carotenóides – CAR, taxa de assimilação líquida de CO_2 – *A*, condutância estomática - gs, taxa de transpiração – *E*, concentração interna de CO_2 – Ci, eficiência intrínseca do uso da água – $_{int}$WUE, rendimento quântico efetivo do PSII – ΦPSII, taxa de transporte de elétrons – ETR, coeficiente de extinção fotoquímica – qP e eficiência quântica de centros abertos de reação PSII – Fv' / Fm'.

4. DISCUSSION

Different physiological responses were observed between soybean lineages after exposure to both drought conditions (Figure 1–6), being the Vx-08-10819 the one that showed the best drought tolerance responses, with emphasis on the photosynthetic traits (Figure 4–6). Additionally, the RWC in the Vx-08-10819 was not changed after the water restriction (Figure 1), keeping the LA and SDW phenotypic traits unchanged during both drought conditions (Figure 2A, 2C), which demonstrates that this lineage has a greater tolerance to drought in the vegetative stage, as well as observed in the reproductive stage (ROSA et al., 2020).

The reduction in leaf water content can result in low turgor pressure, leading to decreased gs and limiting cell expansion (Jaleel et al., 2009), hence causing lessened plant growth and development (Ullah et al., 2017), as observed in the Vx-08-11614 (Figure 2A, 2C–D). Similar results in response to drought were reported in different plant species such as sweet potatoes (YOSHIDA et al., 2020), chili pepper (WIDURI et al., 2020), and cabbage (HAGHIGHI et al., 2020).

The lower Total Chl and carotenoids contents observed in Vx-08-11614 (Figure 3C, 3D, 6) shows a lower efficiency in light absorption and, consequently, a lower transfer of radiant energy to reaction centers under drought (Rosa et al., 2020), which can negatively impact *A*. Chlorophyll and carotenoids contents are a key factor in plant photosynthesis and closely reflects the photosynthetic capacity of plants (TALBI et al., 2020). In addition, the lower carotenoids content decreases the protection of the antenna complex from oxidative damage (Lapaz et al., 2020; Yoshida et al., 2020), since these antioxidants scavenge reactive oxygen species (ROS) to protect the photosynthetic apparatus (ROSA et al., 2020). However, Mesquita et al. (2020) observed a more pronounced decrease in photosynthetic pigments in the tolerant soybean lineage. In fact, reduction in chlorophyll content is attributed as a typical symptom of oxidative stress (Iqbal et al., 2019), indicating that the Vx-08-11614 is more affected by drought stress (ROSA et al., 2020), as shown in Figure 3.

The gs is responsive to almost all external and internal factors related to drought, it represents a highly integrative basis for overall effect of drought on photosynthetic traits (SINGH et al., 2011). In this context, the decrease in gs (Figure 4B) was crucial to optimizing the $_{int}$WUE in both lineages (Figure 4E). Gulias et al. (2012) also found higher $_{int}$WUE in grasses subjected to drought. Additionally, the lower *A* (Figure 4A) observed in the Vx-08-11614 under drought is apparently associated with a marked reduction in gs (Figure 4B), which resulted in lower Ci (Figure 4D) due to the limitation stomatal, as well as a photochemical inhibition (Figure 5A, C–D). Hence, the lower gs reduced Ci, inducing limitations CO_2 assimilation, and causing an imbalance between photochemical activity at PSII and electron requirement for photosynthesis, which increases the susceptibility to photooxidative and oxidative damage to photosystems (Ohashi et al., 2006); this answer explains the reduction in the content of Total Chl e carotenoids in the Vx-08-11614 (Figure 3C, D, 6).

Electron transport rate reduction is a defense strategy against photooxidative damage in plants whose CO_2 fixation is compromised (Yamori, 2016), indicating cumulative effects of biochemical limitations (Mesquita et al., 2020), as noted in the Vx-08-11614 (Figure 5B). Similar results were observed under the same conditions of drought stress imposition, but in the reproductive phenological stage R3 (FEHR; CAVINESS, 1971) by Rosa et al. (2020). In contrast, although gs has also substantially reduced in the Vx-08-10819 (Figure 4B), there was a moderate reduction in *A* and traits of chlorophyll *a* fluorescence were unchanged (Figure 4A, 5), suggesting that the PSII structural integrity of the Vx-08-10819 was not injured by drought (IQBAL et al., 2019).

5. CONCLUSIONS

Relative water content in leaves, LA, and SDW of lineage Vx-08-10819 were not changed after exposure to drought. Besides that, photosynthetic capacity of lineage Vx-08-10819 was less affected than lineage Vx-08-11614 to drought, showing that this lineage is tolerant to this abiotic stress in at vegetative stage V4.

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