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ECOPHYSIOLOGY AND WATER USE EFFICIENCY OF SOYBEAN CULTIVARS UNDER FIELD CONDITIONS

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Abstract
A wide range of soybean cultivars is available on the market and understanding the physiological response and yield of these materials is fundamental to develop new management systems. Thus, the objective of the present study was to assess ecophysiological parameters and yield of soybean cultivars under field conditions. The experiment was carried out on a farm located in the municipality of Açailândia, Maranhão, Brazil. Three commercial cultivars were used (SC1, SC2 and SC3), and gas exchanges, SPAD index, Fv/Fm, photosynthesis index (PI), instantaneous water use efficiency (WUE) and intrinsic instantaneous of the use of water (iWUE) were assessed during the vegetative (V5) and reproductive (R5) stages. In addition, the biomass and production components were obtained. A randomized complete block design was used, with three cultivars and six replications. SC2 obtained the best mean for the photochemical variables. SC2 was more efficient at both development stages in WUE, but the maximum iWUE values were obtained in SC3. The SC2 cultivar obtained the best responses in the main variables analyzed, resulting in a higher yield.

Keywords: Chlorophyll fluorescence. Gas exchange. *Glycine max*. Instantaneous water use efficiency. Photosynthesis.

1. Introduction

Soybean has become an important agricultural commodity because of the wide application of its products for human and animal consumption, and its economic value on the national and international markets (Lima et al. 2017). CONAB (2022) projects for the 2021/2022 harvest 122.8 million tons of grains, 3.8% increase in the planting area and drop yield of 11.1%. The area in the state of Maranhão, Brazil, will crop 1045.9 million ha in this harvest, an increase of almost 4% compared to the 2020/21 harvest.

Due to the importance of the soybean crop in the world context, many cultivars are available on the market, and the choice of the best for a determined region takes into consideration the edaphoclimatic conditions, that are preponderant for a good yield (Gava et al. 2018). Therefore, understanding the mechanisms that alter the plant physiological processes is essential to optimize agricultural crop management. The choice of the cultivar is a crucial factor for the success of the plantation thus the need to know the cultivar response in the various regions is determinant.

The increasing frequency and intensity droughts, associated to high temperatures, due to climatic changes, has caused substantial losses in agricultural areas, so that it has become necessary to develop adaptation strategies capable of mitigating the negative impacts on food offer (Arruda et al. 2015). Species adaptation to the effects climate changes may help in water management under different moisture conditions, which is why water use reflects the complexity of factors involved in plant environment interaction (Silva et al. 2004).

Thus, assessments of the ecophysiological performance of plants allow understanding the performance of the physiological parameters (stomata conductance, transpiration, photosynthesis and leaf temperature), and the response in yield. It is fundamental for development of new management systems to reduce risks of production losser due to the local climatology (Nascimento et al. 2011).

Water use efficiency is an important trait of plants, that characterizes the linking of the water and carbon cycles. Understanding the physiological mechanisms involved in this trait and being able to predict its response in a constantly changing environment it is a big challenge (Knauer et al. 2017). The dependency of the crop yield on water supply results from the water soil plant atmosphere relations, with the balance of two factors that occur at the same time: water conservation and atmospheric CO_2 assimilation. The lag between transpiration, absorption, and water availability in the soil processes cause decrease in yield because it hinders the photosynthesis process (François 2012). Soybean, because it is a plant with C3 carbon metabolism, has less photosynthetic efficiency compared to C4 plants. The superior anatomic and biochemical properties of C4 plants, compared to those with C3 photosynthesis, provide more resilience and control of the photosynthesis activity. especially under adverse conditions, such as heat and drought (Liu et al. 2019).

The objective of the present study was to assess the ecophysiological response of soybean plants cultivated in the Western region of the state of Maranhão and to observe how the environmental conditions interfered in the cultivar growth and development and determine which cultivar was the highest efficient in both water use and yield.

2. Material and Methods

Experimental site and weather conditions

The experiment was carried out on the Farm Reunidas Bola Branca, located in the municipality of Açailândia, Western region of Maranhão state, Brazil (4°42’09” S and 47°37’00” W, 240 m altitude). The regional climate is the Aw subhumid tropical, according to the Köppen classification, with 1334 mm mean annual rainfall and 26°C average temperature. The region has two well-defined seasons: a wet season that is concentrated between November and May and a dry season, between the months of June and October (Correia Filho 2011). The physicochemical characteristics of the soil at 0 – 20 cm deep layer, before installing the experiment, were pH in $CaCl_2$ = 5.0; H+Al=2.5 $cmol_c\ dm^{-3}$; 0 $cmol_c\ dm^{-3}$ Al^{+3}; 3.8 $cmol_c\ dm^{-3}$ Ca^{+2}; 0.9 $cmol_c\ dm^{-3}$ Mg^{+2}; 0.25 $cmol_c\ dm^{-3}$ K^{+}; 2.11 mg dm^{-3} (Mehlich); 2.9 g dm^{-3} organic matter and 64% saturation by bases; clay =700 g kg^{-1}; silt =75 g kg^{-1} and sand =225 g kg^{-1}.

Climatic variables

The environmental conditions were monitored with a meteorological mini station (WatchDog, series 2000, model 2900ET, Spectrum Technologies, Inc., Illinois, USA) and the data collected (average temperature, maximum and minimum and average temperature, relative air humidity, photosynthesis active radiation and rainfall) were stored during the day at 60-minute intervals. The air vapor pressure deficit (VPD) was calculated according to the equation by Jones (1992).

During the experimental period, the maximum temperature was approximately 33°C, the minimum was 20°C and the average temperature was 25°C. The average relative humidity was 84%, the accumulated recorded rainfall was 946.5 mm (23/12/2017 to 08/04/2018, planting and harvest, respectively), with the highest volume in the month of March (234.7 mm) (Figure 1A). The highest DPV_{air} value recorded was 3.0 kPa. The photosynthetically active radiation had maximum values of 1799 µmol m^{-2} s^{-1} in V5 and 1794 µmol m^{-2} s^{-1} in R5 (Figure 1B).

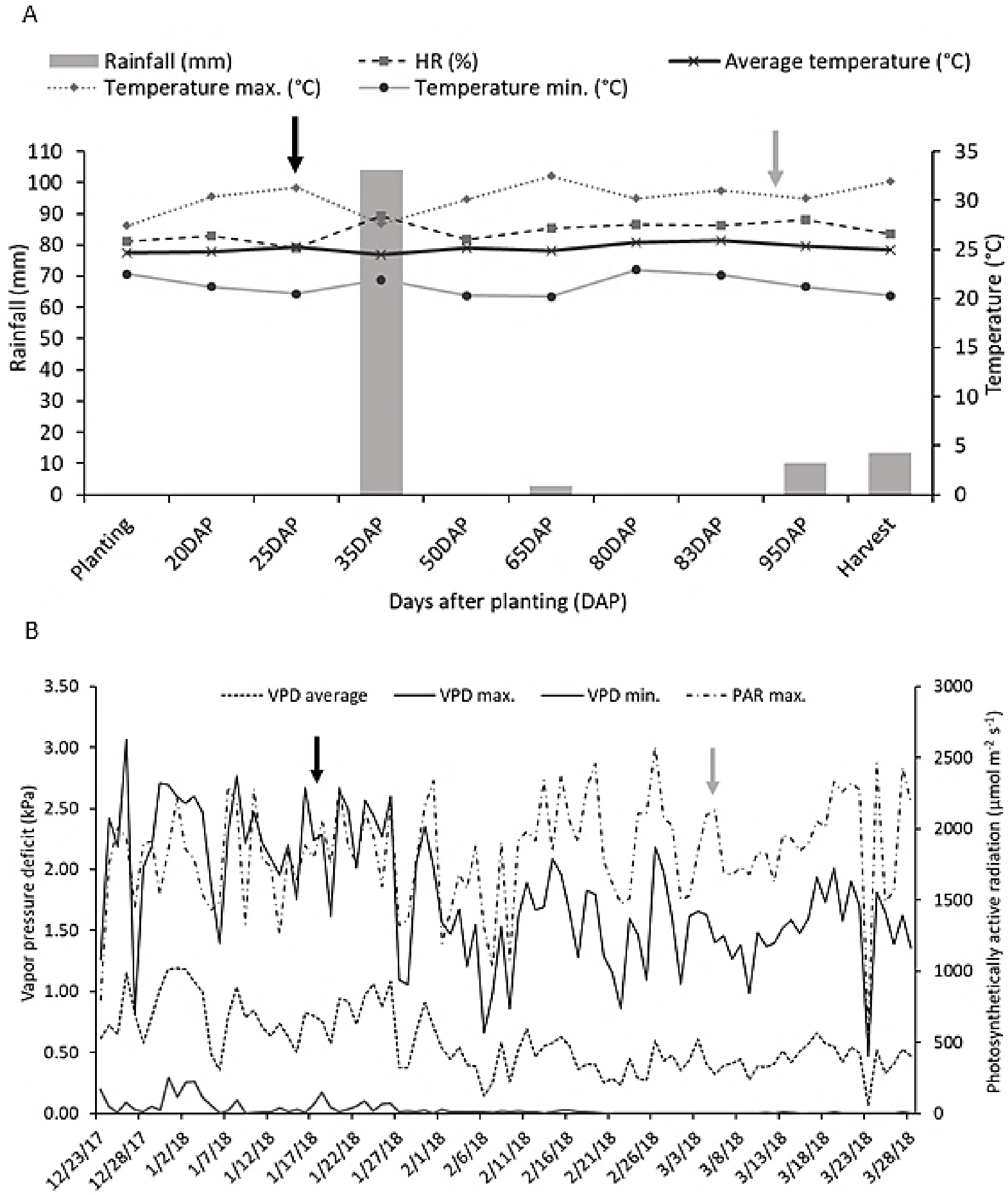

Figure 1. Data climate collected during the experimental period, crop 2017/18, in Açailândia, Maranhão, Brazil. A – Rainfall, humid relative (HR) and temperature averange, maximum and mininum; B – Vapor pressure deficit (VPD) and photosynthetically active radiation. Black arrows: indicate evaluation time at vegetative (V5), and gray arrows: indicate evaluation time at reproductive (R5).

Experimental design

The experiment was set up in december 2017. The treatments consisted of combining the three commercial soybean cultivars, designated in the present study as SC1, SC2 and SC3, and two crop development phases V5 (fifth node – fourth completely opened trifoliate leaf) and R5 (start of grain swelling – grain 3 mm long in a pod on one of the last four nodes of the stem, with a completely opened leaf) (Faria et al. 2007).

A randomized complete block design was used with six replications. The plot consisted of 54.5 m long rows, spaced at 0.50 m. The plot useful area was 6 m² and the two side rows and 0.25 m of each extremity of the central rows served as border.

Measurements

Growth evaluation

The biometric analyses were made on three plants per plot at 15-day intervals (20, 35, 50, 65, 80 and 95 days after planting-DAP). At these times, the plant height was measured between the soil surface and the tip bud, and the diameter was measured at the base of the stem with a digital pachymeter (digital steel pachymeter, 150 mm, Stainless).

The specific leaf mass (SLM) was quantified at R8. To quantify the SLM, 10 leaf discs of known area were collected from of five leaves on three plants and placed in a forced air circulation chamber at 70°C until constant matter. The SLM was obtained from the ratio between the dry disc matter and the leaf disc area (disc area: 0.26 cm^2).

Ecophysiological measurements

The physiological measurements were taken twice during the cycle, the first at the vegetative stage (V5) and the second at the reproductive stage (R5). The physiological parameters were measured between 07:30 a.m. and 10:00 a.m. and the measurements were made on a completely open leaf located on the upper third of the plant.

The photosynthesis CO_2 assimilates (A) transpiration (E) and stomata conductance (g_s) were determined with a portable Infra-Red Gas Analyzer (IRGA), modelo Li-6400 (LI-COR, Lincoln, NE, USA), coupled to a light source fixed at 1500 µmol m^{-2} s^{-1} photosynthetic photon flow intensity and air flow 500 µmol s^{-1}. One reading was made per plant, on three plants per plot.

The green intensity was estimated using a portable chlorophyll meter, SPAD-502 "*Soil Plant Analiser Development*" (Minolta, Japan) and five readings were made per leaf on 30 plants per plot. Using a non-modulated fluorimeter, model Pocket PEA (*Plant Efficiency Analyser*, Hansatech, King's Lynn, UK), the F_v/F_m ratio was obtained (a single strong light pulse, 1s 3500 µmol m^{-2} s^{-1}, was applied after acclimatization for a period of 20 minutes) (Bolhar-Nordenkampf et al. 1989). The photosynthetic index (PI) was also determined using the non-modulated fluorimeter; one reading was made per plant on three plants per plot.

The instantaneous water use efficiency (WUE) was estimated from the A/E ratio along with the intrinsic instantaneous water use efficiency (iWUE), substituting only the E values by the values of the stomata conductance (*gs*) the agronomic water use efficiency (AWUE) was obtained by the quotient between the grain yield and the total volume of water precipitated in the period of the crop cycle (m^3 ha^{-1}).

Agronomic variables

The plot useful areas were harvested manually, and yield was corrected to 130 g kg^{-1} moisture. Thirty plants were harvested per plot, to quantify the total number of pods (TNP) and the total number of grains (TNG). The mass of 100 grains (MHG) was obtained by assessing eight 100-grain sub-samples following the Rules for Seed Analysis (Brasil 2009). Grain yield (GRY) was determined by weighing all the grains of the plants collected in each plot (6 m², with a total of 36 m² per cultivar).

The plant biomass, shoot dry matter (SDM) was obtained from 30 plants, dried in a forced air circulation chamber at 70°C to constant matter. Next, 0.2 g samples of the dry, ground plant material were submitted to sulfuric digestions and the TNF was determined by the Kjeldahl method, according to Tedesco et al. (1995). The nitrogen content was obtained by multiplying the nitrogen content by the dry plant matter. These data were used to calculate the nitrogen use efficiency (NUE) from the ratio between the dry plant matter and the N content in the plant, according to Hakeem et al. (2011).

Statistical analysis

The data were submitted to analysis of variance (ANOVA). The Tukey test was used to compare the cultivar means and the crop development phases were compared by the F test. ($p < 0.05$) was used for all the statistical analyses. Principle component analysis using the physiological data and the productive components was used to understand the relationships between the variables. The R software was used to carry out the statistical analysis (package *ExpDes.pt* and function *princomp*).

3. Results

Growth variables

There was significant difference ($p < 0.05$) among the soybean cultivars studied for the variables: plant height, stem diameter and specific leaf mass. SC1 presented the highest growth rate, with a mean of 1.26 cm day^{-1} in height and 0.16 cm day^{-1} in diameter (Figure 2A and 2B). There was no statistical difference ($p < 0.05$) for the values of plant biomass, and the among-cultivars mean was 10.25 g $plant^{-1}$. SC3 presented the highest mean for MFE (0.046 kg m^{-2}) (Figure 2C).

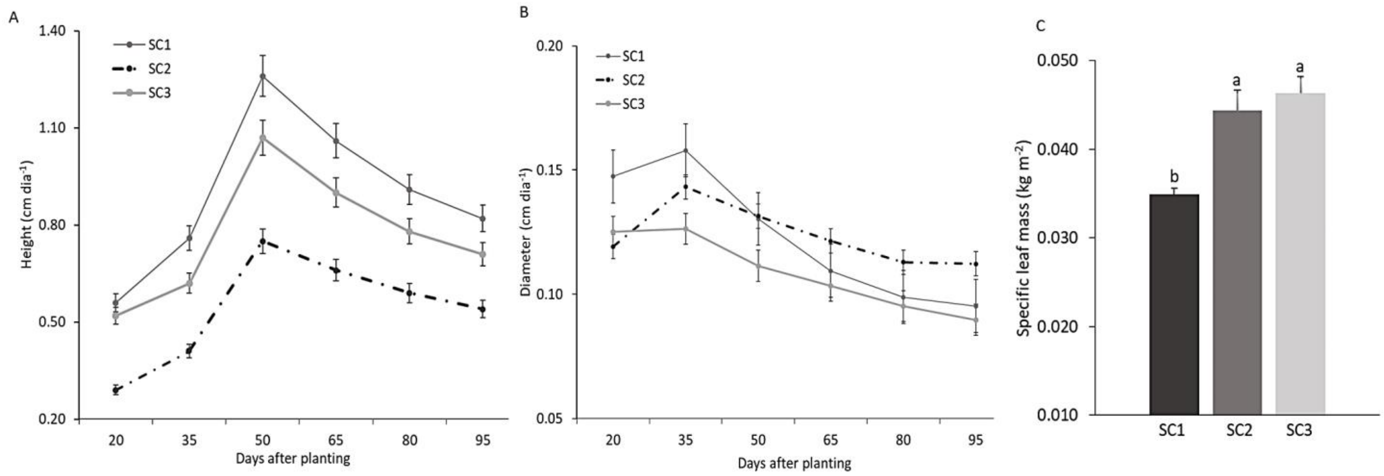

Figure 2. Growth rate variables of soybean plants. A – height, B – diameter, and C – specific leaf mass. Means followed by the same letter not differ by Tukey test ($p<0.05$). Each point and column represent mean the 30 plants.

Gas exchanges

There was no significant difference among the cultivars for photosynthetic CO_2 assimilation (*A*) at the V5 development stage (Table 1) and the general mean was 14.6 µmol m^{-2} s^{-1}. However, at the R5 stage there was significant difference ($p < 0.05$) and the cultivars presented higher means when compared to the V5 stage, especially SC3 that reached 27.2 µmol m^{-2} s^{-1} (Figure 3A). Similar results for *A* in R5 were reported by Djanaguiraman et al. (2019), with values between 21.3 and 28.3 µmol m^{-2} s^{-1}. Transpiration was significantly different among the cultivars at the two stages, V5 and R5 ($p < 0.05$). In V5 the highest transpiration rate was observed in SC1, with 10.68 mmol m^{-2} s^{-1}. At R5, SC2 obtained the lowest transpiration rate, 6.8 mmol m^{-2} s^{-1} (Figure 3B). There was no significant difference for stomata conductance (Table 1) with 0.68 mol m^{-2} s^{-1} general mean.

Photochemical efficiency

SC2 presented the highest means for the maximum quantic the yield of photosystem II, represented by the Fv/Fm ratio, 0.8 and 0.81 for V5 and R5, respectively (Figure 3C). Lopes et al. (2019) worked with soybean genotypes and obtained similar results of values 0.72 - 0.84. Regarding the photosynthetic index, that reflects the state of the photochemical activity of photosystems I and II, an increase was observed in the photochemical activity at R5, compared to V5, with values of 7.62, 1.42 and 0.89 in the cultivars SC2, SC3 and SC1, respectively at R5 (Figure 3D).

Intensity of green

The intensity of green, that represents an estimate of the relative chlorophyll content present in the leaf, increased throughout the cultivar cycle, but there was no significant interaction (Table 1).

Table 1. The significance levels (P-values) for photosynthetic CO_2 assimilation (*A*), transpiration rate (*E*), stomatal conductance (g_s), photosynthetic index (PI), photosystem II efficacy (Fv/Fm), index SPAD, water use efficiency (WUE) and water intrinsic instantaneous use efficiency (iWUE) of soybean plants in two evaluation times at vegetative (V5) and reproductive (R5) phase of soybean development.

Factors	Soybean cultivars (SC)	Evaluation time (ET)	Interaction (SC x ET)
A (µmol CO_2 m^{-2} s^{-1})	0.003099^{**}	$2.2e^{-16***}$	$1.3e^{-05\ ***}$
E (mmol H_2O m^{-2} s^{-1})	$3e^{-06\ ***}$	$3e^{-06***}$	0.004975^{**}
gs (mol H_2O m^{-2} s^{-1})	0.5003^{ns}	0.4843^{ns}	0.1089^{ns}
PI	$1e^{-06\ ***}$	$2e^{-16***}$	$2e^{-16\ ***}$
Fv/Fm	$1e^{-06\ ***}$	0.85978^{ns}	0.03505^{*}
SPAD	0.001817^{**}	$2.2e^{-16\ ***}$	0.205015^{ns}
WUE (µmol CO_2 mmol H_2O)	0.001319^{**}	$2.2e^{-16\ ***}$	0.001260^{**}
iWUE (µmol CO_2 mol H_2O)	0.358579^{ns}	0.004557^{***}	0.472548^{ns}

ns = not significant; * p<0.05; ** p<0,01; *** p<0,001.

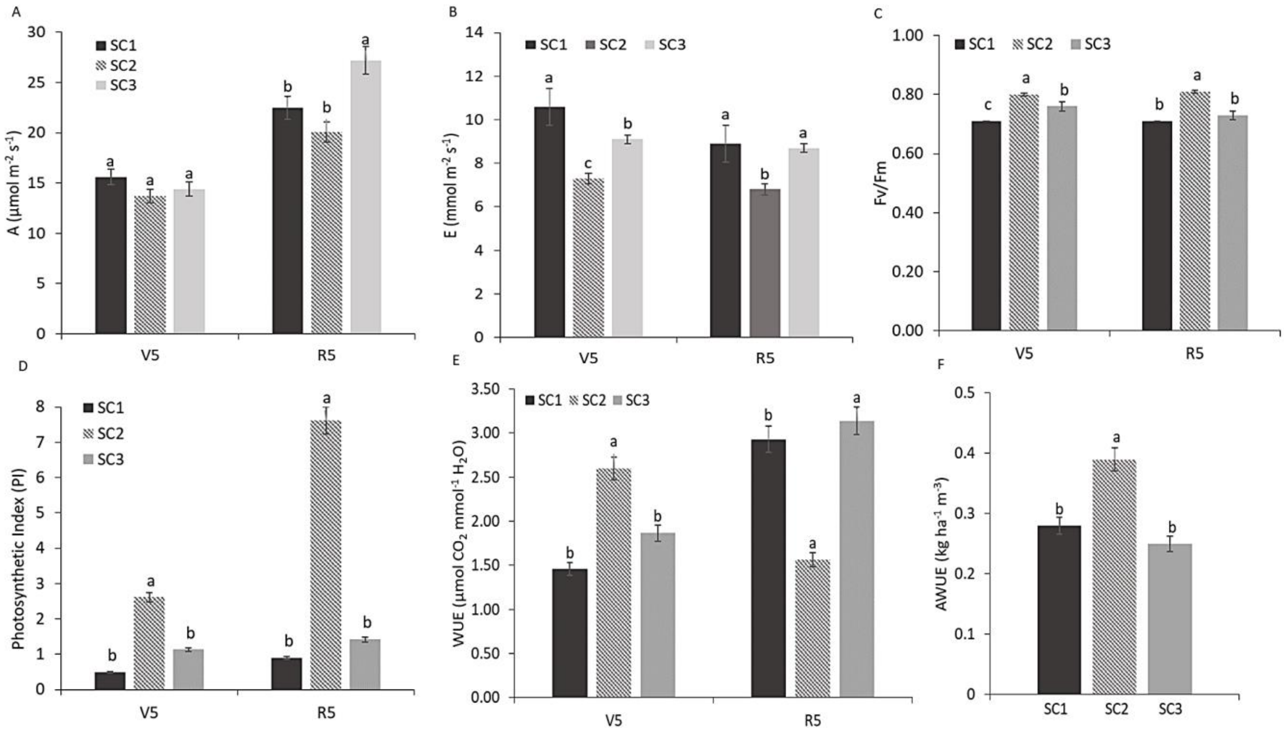

Figure 3. A – Photosynthetic CO_2 assimilation of (*A*), B – transpiration rate – (*E*), C – photosystem II efficacy (Fv/Fm), D – photosynthetic index (PI), E – water use efficiency (E), and F – agronomic water uses efficiency (AWUE) of soybean plants. Means followed by the same letter not differ by Tukey test (p<0.05). Each column represents mean the three plants.

Water use efficiency

The WUE was significantly different between the cultivars. SC2 was the most efficient in V5 with a mean of 2.6 µmol CO_2 $mmol^{-1}$ H_2O. At R5, SC3 was outstanding with 3.14 µmol CO_2 $mmol^{-1}$ H_2O (Figure 3E). These cultivars had the highest values of CO_2 assimilation for each gram of transpired water. There was no significant difference in the maximum iWUE values (Table 1).

The AWUE represents yield in weight per area unit, that the crop is able to produce from the volume of water precipitated during the cycle. SC2 performed best, producing 0.3 kg grain per hectare for each cubic meter water precipitated (Figure 3F), achieving a yield 25 and 35% higher than SC1 and SC3, respectively.

Nitrogen use efficiency

There was significant difference ($p < 0.05$) for nitrogen use efficiency (NUE). SC2 was the most efficient cultivar, producing 38.96 g dry matter for each gram of nitrogen assimilated. SC1 and SC3 obtained, respectively, 36.11 and 24.43 g MS g^{-1} N (Figure 4A).

Production and yield components

There was significant difference for the total number of pods and grains, especially for SC2 (Figure 4B and 4C), that presented values of 69 pods $plant^{-1}$ and 170 grains $plant^{-1}$, while SC1 obtained means of 48 pods $plant^{-1}$ and 101 grains $plant^{-1}$, and SC3 44 pods $plant^{-1}$ and 105 grains $plant^{-1}$. SC3 presented the highest mean for weight of one hundred grains (Figure 4D). Regarding yield, SC2 was the most productive, producing 3698 kg ha^{-1} and was 36% more productive than SC3, that had lower yield (Figure 4E).

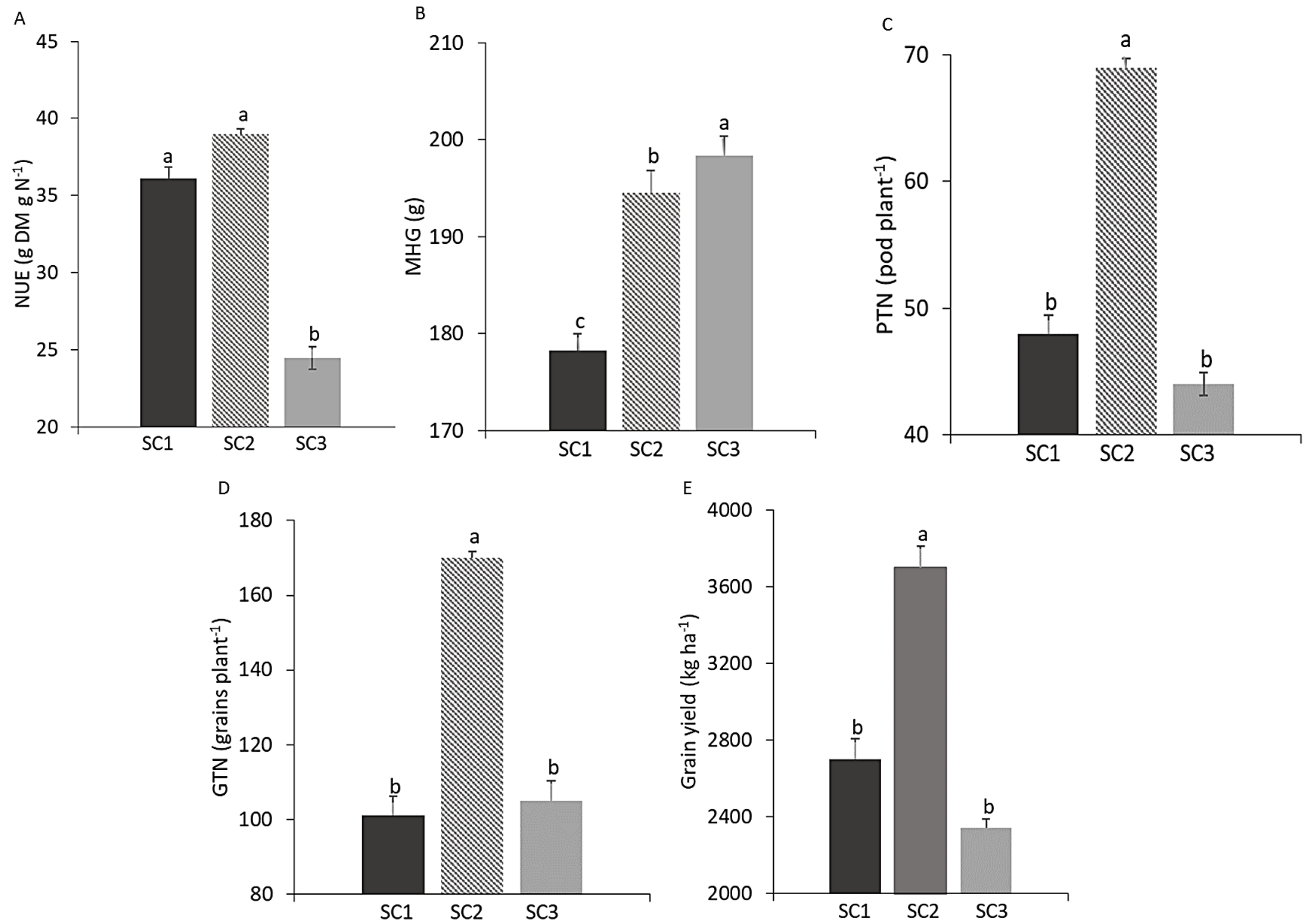

Figure 4. A - Nitrogen use efficiency, B – mass hundred grains, C – pods total numbers, D – grains total numbers, and E – grain yield of soybean plants. Means followed by the same letter not differ by Tukey test ($p<0.05$). Data collected time at reproductive (R5) and each column represent mean the 30 plants.

Principal component analysis

In the principal components analysis, the first axis accounted for 55.2% of the variances observed, while the second axis showed 17.1% of the variances, corresponding to 72.3% of the total variance (Figure 5). The first and second axes give enough information to support the obtained results. The photochemical and production variables accounted for most of the variance in the data, and the gas exchanges correlated negatively with the other variables. Most of these variances are explained by axis 1, and each correlation indicated that the photochemical activity directly influenced the productive response of the SC2 cultivar.

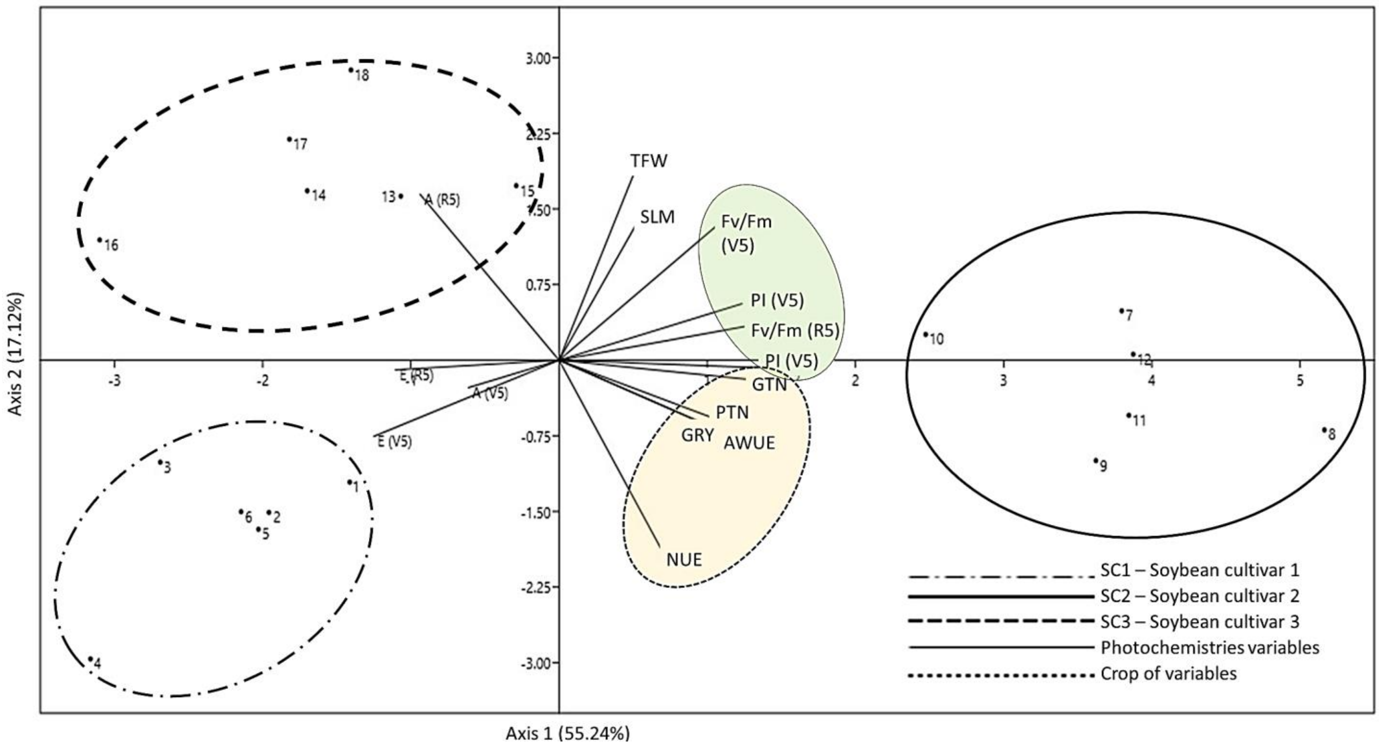

Figure 5. Principal component analysis between physiological (*A* e *E*), photochemical (Fv/Fm e PI) and crop (TGW, SLM, GTN, PTN, AWUE, NUE e GRY) variables at two evaluation times (V5 e R5).

4. Discussion

Photosynthesis CO_2 assimilation (*A*) and stomata conductance (g_s) at V5 stage presented lower values compared to R5. This may have occurred because the assessments in R5 were more favorable, because there was higher light intensity (even if the increase was small) and less VPD_{air} and water was available (Figure 1) due to heavy rainfall on the day prior to the assessment, that may have contributed to a better performance of the cultivars' photosynthesis activity.

The plant tends to reduce stomata conductance in response to a period of water restriction, as a mechanism to limit water loss, that consequently reduces CO_2 assimilation (Nankishore and Farrell 2016). Fenta et al. (2012), studying an 18-day water shortage applied to three soybean cultivars, reported that the photosynthesis level fell on the second day after applying the shortage. These results corroborate with the present study because on the assessment day at stage V5, it had not rained for two days that may have damaged *A* in this assessment.

Cardona-Ayala et al. (2014) studied physiological and biochemical responses in cowpea under water shortage and reported that with reduced soil moisture content there were significant decreases in photosynthesis CO_2 assimilation (*A*), stomata conductance (g_s) and transpiration (*E*). Firmino et al. (2009) also observed that there was significant reduction in net photosynthesis and increased transpiration in soybean plants submitted to water shortage. Because, with limited water availability, less ATP and NADPH are formed and consequently less CO_2 is fixed so that photosystem II (PSII) depends on water to generate chemical energy required to fix CO_2, demonstrating that variations in water availability generate less efficiency in photosystem II (Silva et al. 2015).

The Fv/Fm ratio describes the maximum quantic efficiency of PSII photochemical activity. This ratio has been used to determine disturbances in the photosynthetic system, since its reduction indicates a decline in the PSII photochemical efficiency and damage to the photosynthetic apparatus (Azevedo Neto et al. 2011). In the present study, the photosynthetic apparatus of all the cultivators functioned well throughout the experiment, remaining within the 0.71 - 0.81 range. According to Bolhar-Nordenkampf et al. (1989), plants with 0.70 - 0.85 Fv/Fm values present intact photosynthetic apparatus while less than 0.7 indicates a stressed situation, with consequent reduction in plant photosynthetic potential.

In addition to the Fv/Fm ratio to assess the photochemical condition of the plants, there is the photosynthetic index (PI) that is considered more complete because it integrates three independent components, assessing the activity of photosystems II and I. Strasser et al. (2000) reported that values above 0.5 PI indicate high efficiency of the photosynthetic apparatus. Thus, with the exception of SC1, in the V5 period, that had an index of 0.49, the other cultivars studied presented satisfactory photochemical activity, especially SC2, that obtained the highest values in both periods (2.61 and 7.62 for V5 and R5, respectively) (Figure 3D).

The SPAD index has been used to assess soybean development in several studies (Ferreira et al. 2018; Santos 2018; Gonçalves et al. 2018). Yokoyama et al. (2018) observed positive correlation between the SPAD index and grain yield (41 and 4028 kg ha^{-1}, respectively) in soybean cultivars at stage R5. The authors attributed this to the high demand for photoassimilates in this period for grain formation. SC2 had the highest mean at stage R5, 48.7 at 80 DAP and after this day there was a fall in the index values which occurred due to the senescence period of the plants.

Genetic breeding of soybean has brought various benefits to the crop but, as reported by Serra et al. (2011), the considerable increase in herbicide applications in the same cycle has damaged biological nitrogen fixation, and consequently the availability of this nutrient for the plants. With this, the study of nutrient use efficiency by plants is necessary due to the intensive management there is in the fields. Procópio et al. (2004) assessed nitrogen absorption and use in soybean plants and reported a mean of 37 g MS g^{-1} N. Similar values were observed for SC2 in the present study (Figure 4A). The instantaneous water use efficiency (A/E), and the intrinsic water use efficiency (A/g_s) are obtained from the gas exchanges which express the efficiency with which plants use water at the same time as they assimilate carbon. Purcell et al. (1997) observed that cultivars with higher WUE levels would be capable of maintaining higher biomass production, a result observed in the present study, in SC2. Rosa et al. (2017) observed that high WUE values are characteristics of plants tolerant to low water availability and serve as parameters to indicate the physiological plasticity of the plants to abiotic factors.

According to Berry et al. (2010), plants with high stomata control are more efficient intrinsic water use. This performance was observed in the present study, where SC3 presented the lowest stomata conductance rates and was the cultivar with the best intrinsic water use efficiency. Santos et al. (2017) also reported correlation of reduced stomata conductance with increased iWUE, that according to the authors, indicated carbon absorption with less water loss, contributing to maintaining photosynthesis.

Highlighting the variables that most contributed to the agronomic characteristics, SC2, consequently, presented the largest number of pods and grains per plant. Although SC3 presented the highest MHG, this cultivar was less productive. According to Araújo et al. (2016), the weight of 100 grains is an important variable in the grain quality assessment, but can generate great variability due to the conditions of temperature, light and humidity during the maturation stage in the field.

SC2 obtained the best results for the Fv/Fm ratio, SPAD index and NUE, with best water use efficiency and presented high correlation ($r = < 0.80$) between the photochemical variables and the productive components (Figure 5). With this, it obtained the highest yield among the cultivars studied.

5. Conclusions

The soybean cultivars performed similarly for CO_2 assimilation, transpiration and stomata conductance. SC2 was outstanding for the Fv/Fm ratio, photosynthetic index, SPAD index and nitrogen use efficiency. It was most efficient in water use and made better use of water precipitated during the cycle, with the highest values for instantaneous, intrinsic and agronomic water use efficiency. In the assessments of the agronomic components, SC2 performed better than the other cultivars. This cultivar presented the best physiological response, when compared to the other cultivars, for the climatic conditions to which it was exposed. It expressed all its genetic potential in the reproductive stage, optimizing the use of available resources that resulted in a higher yield.

Authors' Contributions: COSTA, N.B.: acquisition of data, analysis and interpretation of data, drafting the article; OLIVEIRA, M.F.C.: acquisition of data; BRAUN, H.: analysis and interpretation of data; BERELLI, S.S.: review of intellectual content; FIGUEIREDO, F.A.M.A.: review of intellectual content; REIS, F.O.: review of intellectual content; FERRAZ, T.M.: conception and design, analysis and interpretation of data, drafting the article. All authors have read and approved the final version of the manuscript.

Conflicts of Interest: The authors declare no conflicts of interest.

Ethics Approval: Not applicable.

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