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Interaction of Carbon Dioxide Enrichment and Soil Moisture on Photosynthesis, Transpiration, and Water Use Efficiency of Soybean

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Abstract

Soybean (*Glycine max* (*L.*) Merrill) is one of the most important oil and protein sources in the world. Interactive effect of elevated carbon dioxide (CO_2) and soil water availability potentially impact future food security of the world under climate change. A rhizotron growth chamber experiment was conducted to study soil moisture interactions with elevated CO_2 on gaseous exchange parameters of soybean under two CO_2 concentrations (380 and 800 $\mu mol \cdot mol^{-1}$) with three soil moisture levels. Elevated CO_2 decreased photosynthetic rate (11.1% and 10.8%), stomatal conductance (40.5% and 36.0%), intercellular CO_2 concentration (16.68% and 12.28%), relative intercellular CO_2 concentration (17.4% and 11.2%), and transpiration rate (43.6% and 39%) at 42 and 47 DAP. This down-regulation of photosynthesis was probably caused by low leaf nitrogen content and decrease in uptake of nutrients due to decrease in stomatal conductance and transpiration rate. Water use efficiency (WUE) increased under elevated CO_2 because increase in total dry weight of plant was greater than that of water use under high CO_2 conditions. Plants under normal and high soil moisture levels had significantly higher photosynthetic rate (7% to 16%) favored by optimum soil moisture content and high specific water content of soybean plants. Total dry matter production was significantly high when plants grown under elevated CO_2 with normal (74.3% to 137.3%) soil moisture level. Photosynthetic rate was significantly and positively correlated with leaf conductance and intercellular CO_2 concentration but WUE was significantly negatively correlated with leaf conductance, intercellular CO_2 concentration and transpiration rate. However, the effect of high CO_2 on plants depends on availability of nutrients and soil moisture for positive feedback from CO_2 enrichment.

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Keywords

Elevated Carbon Dioxide, Evaporation, Interactions, Photosynthetic Rate, Soil Moisture, Soybean, Water Use Efficiency

1. Introduction

Soybean (*Glycine max* (*L.*) Merrill) is the world agricultural economy grown primarily for oil extraction and for use as a high protein meal for animal feed [1]. The world population is expected to reach nine billion people by 2050 and production of food should increase by 70% to ensure food security, which should be achieved through increase in productivity [2]. The soybean plants show a series of changes in their morphology, physiology, and biochemistry, negatively affecting their growth which can reduce productivity by 50% [3].

The increasing atmospheric carbon dioxide (CO_2) concentration have direct and indirect effects on crop plants but CO_2 is often a limiting resource in plant canopies, and it's expected to increase photosynthetic rate, plant productivity, and water use efficiency (WUE) by reducing stomatal aperture and/or number per unit leaf area and their by decrease in transpiration [4]-[30]. However, the long-term response remains uncertain due to increase in incidence of extreme weather events [29] [31]-[36] such as drought, heat waves, and heavy precipitation and floods, making crop production more unpredictable and difficult. Yields of most agricultural crops increased under elevated CO_2 concentrations; productivity increases are in the range of 15% to 41% for C3 crops and 5% to 10% for C4 crops [5] [8] [29] [37]. Increased photosynthesis and associated changes in morphology [5] [20] [38] in response to elevated CO_2 increased soybean yield by 24% - 37% [39] [40] and interactions of other climate change factors on plants [41] showed alterations both in physiology, growth, and development crops such as soybean [39], cotton [42], and many other crops [27]. Transpiration is a vital component in soil-water-plant relationship and is of particular importance in studying possible interactions of elevated CO_2 and water supply in terms of plant water use and WUE. The effect of elevated CO_2 concentrations on crops varies under different soil moisture regimes [43]. However, data on the interactive effects of CO_2 and soil moisture on plants are scarce and often contradictory [44]. Previous studies claim that the percentage increase in plant growth due to elevated CO_2 is generally not reduced by water stress [16] [45] whereas the results of many other theoretical projections and field or greenhouse experiments suggest that the relative effects of CO_2 enrichment on plants are constrained by less than optimal levels of soil moisture [5] [24] [46]-[51].

The altered physiological and gas exchange characteristics of crop plants with climate change [52] [53] and coupled with shifts in regional scale rainfall patterns leading to decreased soil water availability in some areas of the world [33] [34] has far-reaching implications particularly in arid and semi-arid regions where water is a critical consideration affecting both growth and development of crops and ultimately impacting yield and food security [54] [55]. In this study, we grew soybean under two CO_2 concentrations and three soil moisture levels, and focused on the interactive effects of elevated CO_2 and soil moisture levels on canopy photosynthetic CO_2 uptake, canopy transpiration, water use efficiency, intercellular CO_2 concentration, and growth of soybean plants during vegetative growth stages.

2. Materials and Methods

2.1. Environment

The experiment was conducted in the controlled environmental conditions under rhizotron chambers at USDA-ARS National Laboratory for Agriculture and Environment (NLAE) in Ames, Iowa, USA. More details of operation and control of rhizotron chambers have been described by [56] [57]. The dimension of each soil monolith is 1 by 1 by 1.5 m deep and the soil type is Monona silt loam soil (fine-silty, mixed mesic Typic Hapludoll) from southwestern Iowa. Each rhizotron growth chamber consists of three soil monoliths. Chambers are similar to a standard plant growth chamber and have microprocessor control of temperature, humidity, and lighting such that specific diurnal, weekly, and seasonal environmental patterns can be programmed. Soil water content of the monoliths also can be monitored and controlled.

Treatment consists of two levels of CO_2 concentration (380 and 800 $\mu mol \cdot mol^{-1}$) and three soil moisture levels (Low, Normal and High) which were studied in the controlled rhizotron environmental condition. Each rhizotron chamber was assigned with a particular level of CO_2 concentration where one chamber with ambient CO_2 level of 380 µmol·mol^{-1} and another with elevated CO_2 level of 800 µmol·mol^{-1}. In each rhizotron chamber, three soil moisture regimes *viz.*, low (5 mm), normal (7.5 mm) and high (10 mm) were imposed. Soybean genotype namely S 21-N6 planted in each soil moisture level (soil monolith) at 60 cm between two rows by opening small furrow of 5 cm depth and placing soybean seeds at 10 cm apart on 25 Oct. 2011. After sowing, each soil monolith was irrigated to 80% field water capacity (FWC) and uniform soil moisture was maintained in the entire soil profile by daily watering to all the monoliths for initial 15 days after planting (DAP) since these rhizotron monoliths were dry before. Two rhizotron chambers were maintained at maximum temperature of 25˚C and minimum of 15˚C, and at 380 µmol·mol^{-1} CO_2 until 50% seedling emergence. Environmental variables viz., CO_2 concentration, temperature and light intensity inside each chamber were continuously monitored and temperature and light were automatically adjusted by the computer to simulate diurnal variations typical of a day. Temperature and light intensity were programmed to be the same between chambers. Only CO_2 was varied between chambers, one with ambient CO_2 and another with elevated CO_2. The environmental sensors and controlling systems of the two chambers were calibrated before the commencement of the experiment and environmental variables were continually monitored at one minute samples and 15 minutes averages during the entire course of experiment in order to minimize the variance induced by the between-chamber heterogeneity of environmental conditions. Photosynthetically active radiation inside the growth chambers was maintained approximately at 280 - 350 µ·mol·m^{-2}·s^{-1} during the course of the experiment.

2.2. Imposition of Treatments

The soil moisture treatments viz., low (5 mm), Normal (7.5 mm) and High (10 mm) were imposed from 15 DAP *i.e*., on 08 Nov 2011 and frequency of watering was twice in a week (Friday and Tuesday). Water was measured and applied to each soil monolith by plastic rose cane as per the soil moisture treatments. Hand weeding was done on 11 Nov 2011. Elevated CO_2 level was maintained in one of the chamber after 50% seedling emergence by automatically injecting CO_2 into the chamber and the level in the chambers was controlled using a CO_2 delivery system and chamber vents. An individual LICOR infrared gas analyzer (LI-800 Gas Hound CO_2 Analyzer, LI-COR, NE, USA) was used to monitor CO_2 levels at each chamber independently. Soil water content was monitored at weekly intervals with a neutron probe through an access tube positioned in the center of each monolith.

2.3. Measurements

For each growth analysis harvest, above- and below-ground growth measurements were assessed by destructive sampling technique of two plants (first and second sampling) and five (final sampling) randomly selected from each row in each soil monolith to measure the individual plant components. Samplings were done at 29, 44 and 58 DAP. Number of leaves per plant, total leaf area (cm^2·plant^{-1}), total above-ground dry mass per plant (g·plant^{-1}), and leaf and stem dry mass (g·plant^{-1}) were determined for all stages. Number of pods and dry weight of pods per plant were measured at final harvest. Leaf area was measured using the LI-3100 leaf area meter (LI-COR, Lincoln, NE). All components wise fresh weights were taken and dry weights were obtained following oven-drying to constant weight at 65˚C. Total above-ground dry biomass for each plant was obtained by adding all plant components. These values were then used for statistical and growth analysis. The specific leaf area (SLA) (cm^2·g^{-1}), leaf area ratio (LAR) (cm^2·g^{-1}) and leaf weight ratio (LWR) (g·g^{-1}) were calculated for each sampling date as the ratio of leaf area to leaf biomass, leaf area to above-ground biomass and leaf biomass to total plant above-ground biomass, respectively.

2.4. Gas Exchange Characteristics

Measurements of net CO_2 assimilation rate (A), transpiration (E), stomatal conductance (gs), intercellular CO_2 concentration (Ci), were made on fully expanded youngest five leaves of soybean plants using LI-6400 Portable Photosynthesis System (Li-Cor, Lincoln, NE). Two measurements were made at 42 and 47 DAP after 72 h and 24 h of watering, respectively as per the soil moisture treatments. Measurements were performed from 14.05 to 15.12 h at 42 DAP and 12.10 to 13.12 h at 49 DAP with the following specifications/adjustments, molar flow of air per unit leaf area 499.2 μ·mol·m^{-2}·s^{-1}, atmospheric pressure 99.7 kPa, temperature of leaf ranged from 31.77˚C to 33.39˚C (at 42 DAP) and 29.3˚C to 32.7˚C (at 47 DAP), ambient temperature ranged from 32.24˚C to 33.85˚C (at 42 DAP) and 29.2˚C to 32.2˚C (at 47 DAP), reference CO_2 concentration was 370 μ·mol·mol^{-1}. Water use efficiency was calculated as CO_2 assimilation rate to transpiration, and intrinsic WUE as CO_2 assimilation rate to stomatal conductance.

2.5. Statistical Analysis

Statistical analysis was conducted by using analysis of variance (ANOVA) (Web Based Agricultural Statistics Software Package (WASP-2)). Effects of CO_2, soil moisture levels, and interactions were tested using the least significant difference tests at P = 0.05. Correlation between fresh weight of soybean plant and various gas exchange parameters were also analyzed. Data at each observational date were analyzed separately. Results are presented in tabular and graphical representation with the standard error bars.

3. Results

3.1. Photosynthetic Rate or Net Assimilation Rate

Net assimilation rate (NAR) of soybean was highly significant due to CO_2 levels and decrease in photosynthetic rate by 11.1% and 10.8% under elevated CO_2 compared to ambient CO_2 level at 42 and 47 DAP ($P \leq 0.01$), respectively (**Table 1** & **Figure 1**). Plants under normal and high soil moisture levels shows significantly high assimilation rate and it was high by 7% to 11.6% at 42 DAP ($P \leq 0.05$), and 11.7% to 16.0% at 47 DAP ($P \leq 0.01$), over plants under low soil moisture level. On the other hand, statistical analysis shows that there was significant interaction effect between CO_2 and soil moisture levels on NAR both at 42 and 47 DAP ($P \leq 0.05$). Significantly low NAR was under elevated CO_2 with normal soil moisture level (11.6%) at 42 DAP, normal (11.7%) and high soil moisture level (16.0%) at 47 DAP compared to low soil moisture level. Results of this study also revealed that plants had high NAR at 47 DAP compared to 42 DAP.

3.2. Stomatal Conductance

Leaf stomatal conductance of soybean was extremely significant due to CO_2 levels at both 42 and 47 DAP ($P \leq 0.001$). Conductance was high by 40.5% and 36% under ambient CO_2 in comparison to elevated CO_2 level at 42 and 47 DAP, respectively (**Table 1** & **Figure 1**). No significant effect of soil moisture levels and interaction between CO_2 and soil moisture levels on leaf stomatal conductance. However, conductance was high under normal soil moisture level (14.7% and 11.2% under low and high soil moisture level, respectively) at 42 DAP and where at 47 DAP, high soil moisture level had high leaf conductance by 27% and 11.5% compared to low and normal soil moisture levels, respectively.

3.3. Intercellular CO_2 Concentration

Plants grown under elevated CO_2 had low intercellular CO_2 concentration (16.68% & 12.28%) at 42 and 47

Table 1. Statistical results of gas exchange parameters of soybean genotypes influenced by [CO_2] (elevated & ambient) and soil moisture levels (L: Low, N: Normal & H: High) and their interaction effects at 42 and 47 DAP [Assimilation rate (A), Stomatal conductance (gs), Intercellular CO_2 (Ci), Transpiration rate (E), water use efficiency (WUE), relative intercellular (CO_2) concentration (Ci/Ca), and intrinsic water use efficiency (A/gs)].

Treatment	A		gs		Ci		E		WUE		Ci/Ca		A/gs	
	DAP													
	42	47	42	47	42	47	42	47	42	47	42	47	42	47
CO_2 level (A)	**	**	***	***	**	NS	***	***	***	*	***	NS	***	NS
Soil moisture (B)	*	**	NS	NS	NS	NS	NS	*	NS	NS	NS	NS	NS	NS
AXB	*	*	NS	NS	NS	NS	NS	NS	*	NS	NS	NS	NS	NS

*, **, *** = significant at 0.05, 0.01, and 0.001 levels, respectively; NS = not-significant.

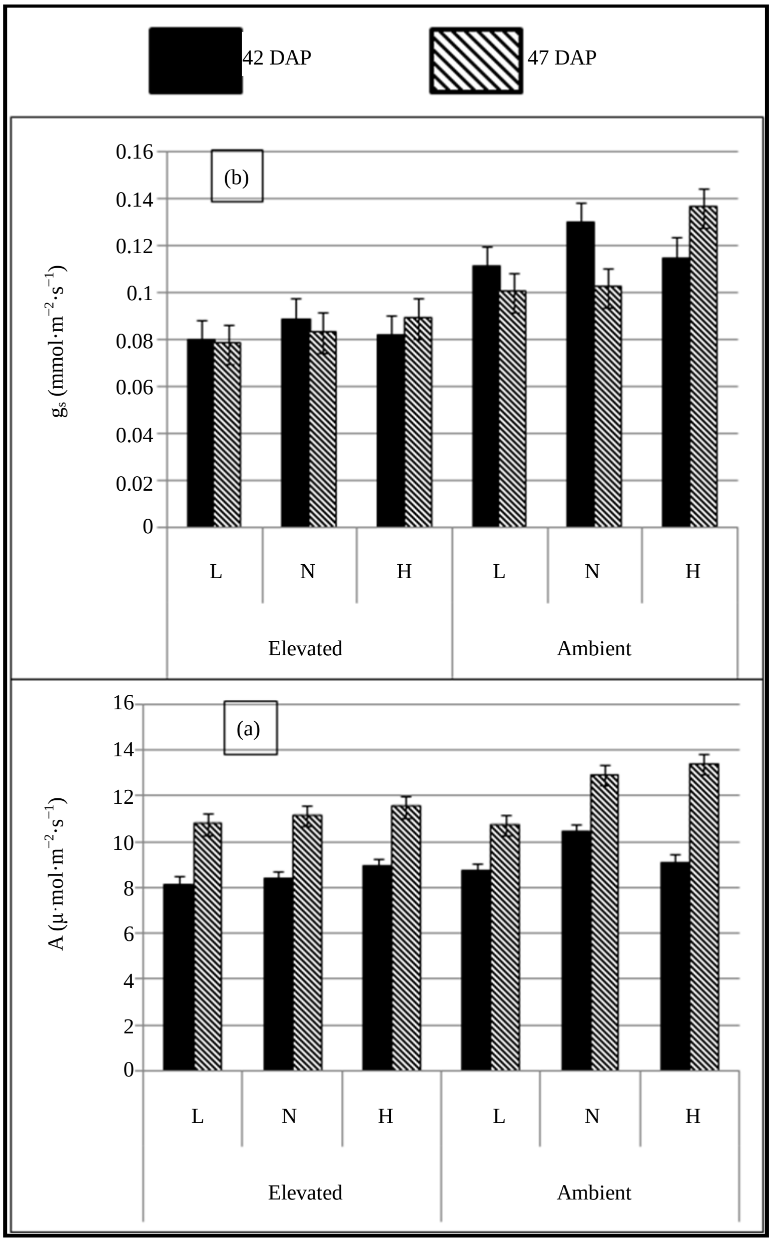

Figure 1. (a) Assimilation rate (a), and (b) stomatal conductance (gs) of soybean under (CO_2) (elevated & ambient) and soil moisture levels (L: Low, N: Normal & H: High).

DAP but it was significant only at 42 DAP ($P \leq 0.01$) (**Table 1** & **Figure 2**). Soil moisture levels and interaction effect of CO_2 and soil moisture were not significant at both 42 and 47 DAP. However, plants under ambient CO_2 with normal soil moisture at 42 DAP and with low soil moisture at 47 DAP showed relatively high intercellular CO_2 concentration compared to elevated CO_2 with low to high soil moisture content. On the other hand, plants had high intercellular CO_2 concentration (72%) at 42 DAP compared to 47 DAP.

3.4. The Relative Intercellular CO_2 Concentration

The relative intercellular CO_2 concentration (Ci:Ca intercellular CO_2 concentration:ambient CO_2 concentration) was extremely significant due to CO_2 levels only at 42 DAP ($P \leq 0.001$) and it was significantly low under elevated CO_2 level by 17.4% and 11.2%, respectively at 42 and 47 DAP compared to plants under ambient CO_2

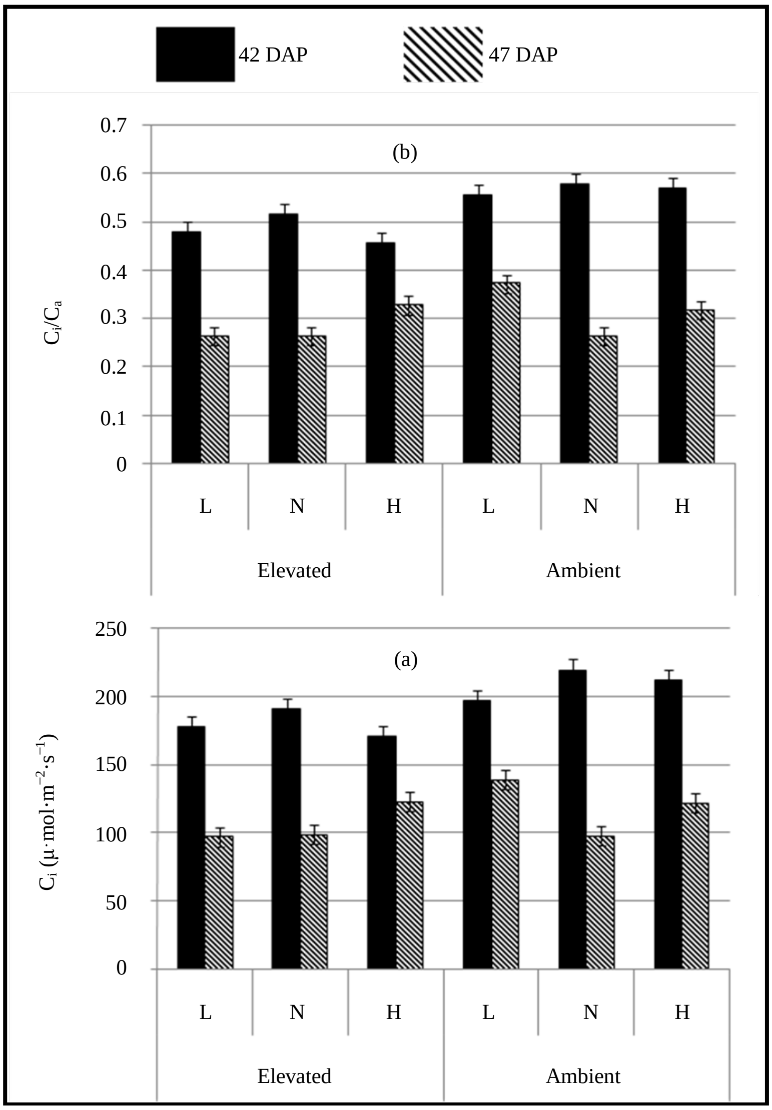

Figure 2. (a) Intercellular [CO_2] concentration (Ci) and (b) relative intercellular (CO_2) concentration (Ci/Ca) of soybean under (CO_2) (elevated & ambient) and soil moisture levels (L: Low, N: Normal & H: High).

level (**Table 1** & **Figure 2**). Soil moisture levels and interaction between CO_2 and soil moisture levels were not significant. However, results of the study shows that plants had high relative intercellular CO_2 concentration under ambient CO_2 level with normal soil moisture at 42 DAP and with high soil moisture at 47 DAP. Plants had high relative intercellular CO_2 concentration by about 76% at 42 DAP compared to that of 47 DAP.

3.5. Transpiration and WUE

Transpiration rate was extremely significant due to CO_2 levels both at 42 and 47 DAP ($P \leq 0.001$). Transpiration rate was low in plants under elevated CO_2 level by 43.6% and 39% over ambient CO_2 at 42 and 47 DAP, respectively (**Table 1** & **Figure 3**). Soil moisture levels significantly affected transpiration rates only at 47 DAP ($P \leq 0.01$) and it was high under high soil moisture level by 26% and 18% compared to low and normal soil moisture levels. However, interaction effects of CO_2 and soil moisture levels were not significant. On an average, high transpiration rate of about 76.4% at 47 DAP compared to 42 DAP.

Plants under elevated CO_2 had significantly high WUE of 29% and 14% at 42 ($P \leq 0.001$) and 47 DAP ($P \leq 0.01$), respectively compared to ambient CO_2 level. Water use efficiency not influenced significantly by soil

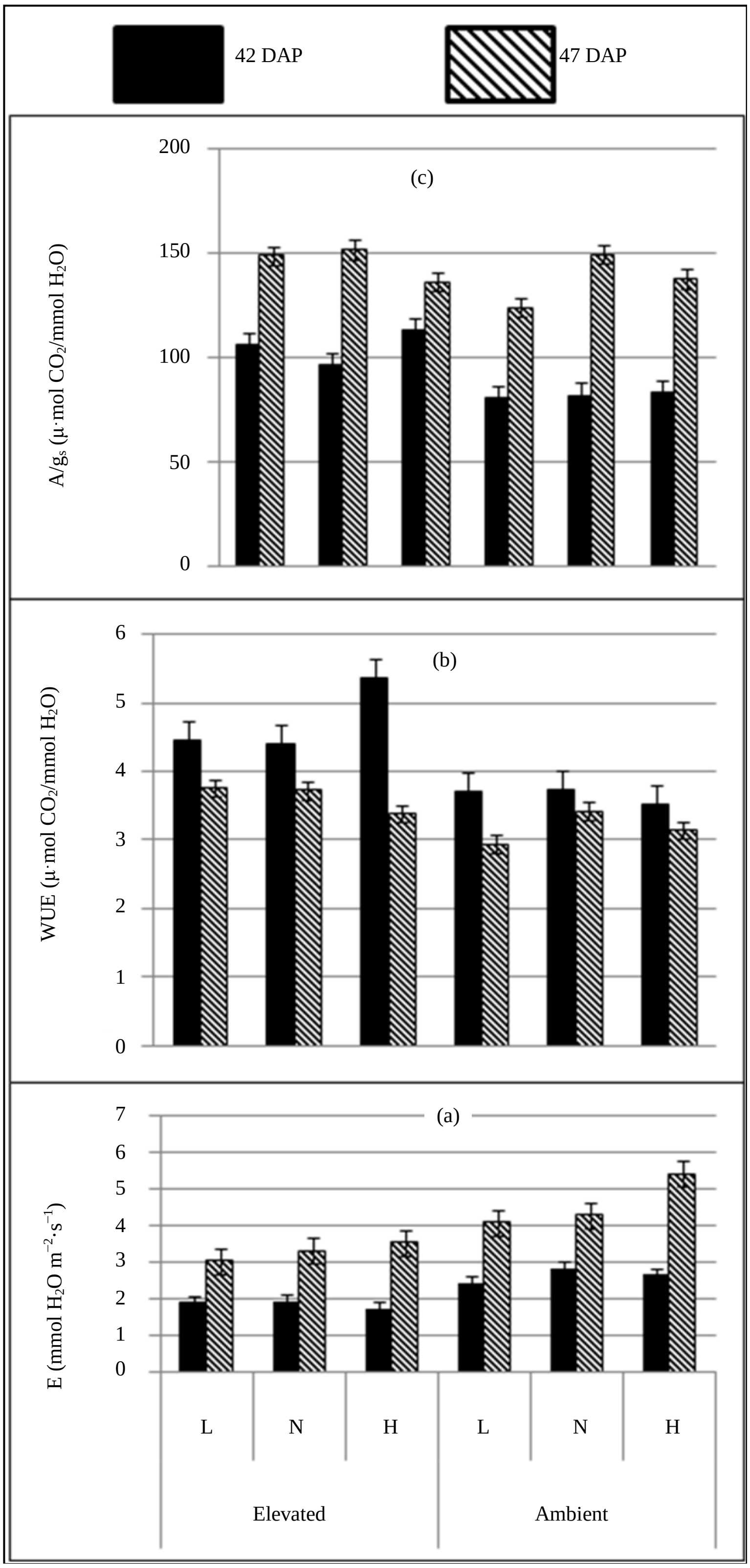

Figure 3. (a) Transpiration rate (E), (b) Water use efficiency (WUE) and (c) intrinsic water use efficiency (A:gs) of soybean under (CO_2) (elevated & ambient) and soil moisture levels (L: Low, N: Normal & H: High).

moisture levels. Statistical analysis revealed that, interaction effect of CO_2 and soil moisture levels were significant only at 42 DAP ($P \leq 0.05$) and where plants under elevated CO_2 with high soil moisture level had high WUE. Relatively, WUE was high by 27.5% at 42 DAP compared to that of 47 DAP.

3.6. Intrinsic Water Use Efficiency (A/gs)

Intrinsic water use efficiency (A/gs) was extremely significant for CO_2 levels at 42 DAP ($P \leq 0.001$) and it was high in plants under elevated CO_2 level at 42 and 47 DAP (28.02% and 6.3%) compared to ambient CO_2 level (**Table 1** & **Figure 3**). On the other hand, no significant effect of soil moisture and interaction between CO_2 and soil moisture levels on intrinsic water use efficiency of plants.

3.7. Total Dry Weight of Plants

Total dry weight of plants differed significantly due to CO_2 and soil moisture level only at later stage of crop growth (58 DAP). Plants under elevated CO_2 produced significantly high total dry matter (55%) compared to plants under ambient CO_2 level at 58 DAP ($P \leq 0.001$) (**Figure 4**). At 29 DAP, total dry matter production was high in plants under elevated CO_2 but at 44 DAP it was high under ambient CO_2 level. At all the sampling dates, plants under normal soil moisture level had maximum dry matter but it was significant only at later stage of the crop (58 DAP) ($P \leq 0.002$). Plants under normal soil moisture level produced 56.6% and 50.1% high total dry matter compared to low and high soil moisture levels, respectively at 58 DAP. Interaction effect of CO_2 and soil moisture levels was significant for total dry matter at early (29 DAP) and at later stage (58 DAP) of crop growth. At 29 ($P \leq 0.01$) and 58 DAP ($P \leq 0.05$), total dry matter production was significantly high when plants grown under elevated CO_2 with low (9.4% to 34.6% high) and with normal (74.3% - 137.3% high) soil moisture levels, respectively.

Correlation coefficient (r) of total fresh weight of soybean plant was significantly positively correlated with net assimilation rate ($r = 0.294^*$, $P \leq 0.05$), leaf conductance ($r = 0.286^*$, $P \leq 0.05$) and transpiration($r = 0.0.266^*$, $P \leq 0.05$) at 42 DAP (**Table 2**). Net assimilation rate showed a significant positive correlation with leaf conductance ($r = 0.0.467^*$ & $r = 0.643^*$, $P \leq 0.05$) and intercellular CO_2 concentration at both 42 and 47 DAP. However, WUE was significantly negatively correlated with leaf conductance ($r = -0.691^*$ & -0.833^*, $P \leq 0.05$), intercellular CO_2 concentration ($r = -0.757^*$ & -0.988^*, $P \leq 0.05$) and transpiration rate ($r = -0.721^*$ & -0.837^*, $P \leq 0.05$). The relative intercellular concentration CO_2 significantly positive correlation with leaf conductance, intercellular CO_2 concentration and transpiration rate but significantly negative correlation with WUE at both 42 and 47 DAP.

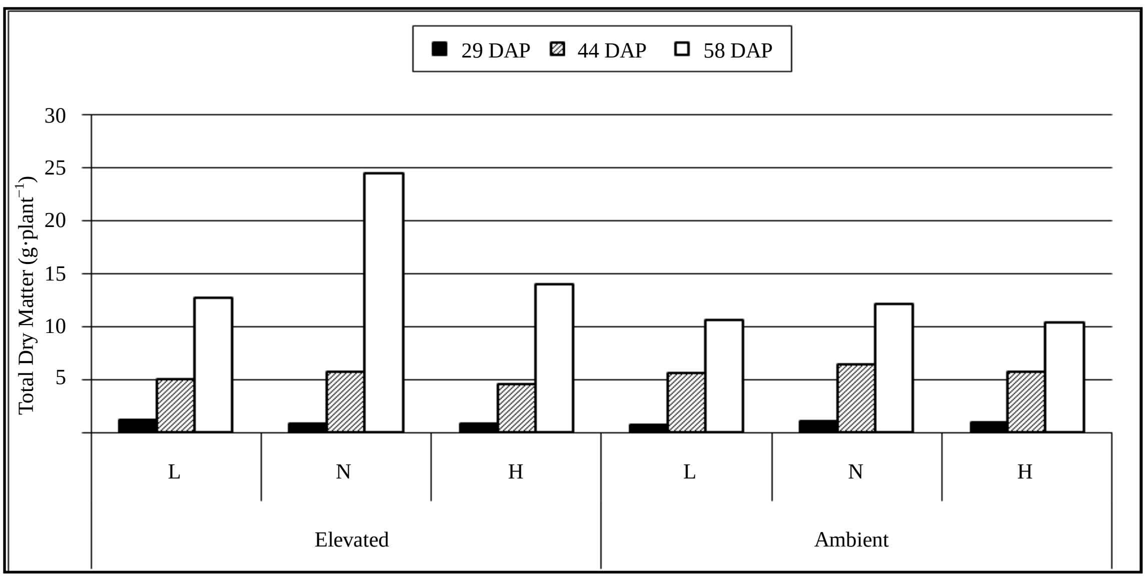

Figure 4. Total dry matter production ($g \cdot plant^{-1}$) of soybean under elevated & ambient (CO_2) with three soil moisture levels (L: Low:,N: Normal & H: High) at 29, 44, and 58 DAP.

Table 2. Correlation coefficient (r) of total fresh weight of plant versus different gaseous exchange parameters at 42 (72 h of watering) and 47 DAP (24 h of watering) of soybean due to (CO_2) and soil moisture levels during day.

	DAP	A	gs	Ci	E	WUE	Ci/Ca	A/gs
Total Fresh Weight	42	0.294*	0.286*	0.040NS	0.266*	−0.055NS	0.062NS	−0.097NS
	47	0.08NS	0.134NS	0.014NS	0.143NS	−0.023NS	0.018NS	−0.009NS
A	42	-	0.467*	0.001NS	0.462*	0.245NS	−0.148NS	0.196NS
	47	-	0.643*	0.395*	0.673*	−0.429*	0.384*	−0.404*
gs	42	-	-	0.695*	0.977*	−0.691*	0.748*	−0.743*
	47	-	-	0.816*	0.999*	−0.833*	0.817*	−0.828*
Ci	42	-	-	-	0.676*	−0.757*	0.945*	−0.796*
	47	-	-	-	0.819*	−0.988*	0.995*	−0.991*
E	42	-	-	-	-	−0.721*	0.716*	−0.729*
	47	-	-	-	-	−0.837*	0.802*	−0.812*
WUE	42	-	-	-	-	-	−0.903*	0.968*
	47	-	-	-	-	-	−0.984*	0.986*
Ci/Ca	42	-	-	-	-	-	-	−0.956*
	47	-	-	-	-	-	-	−0.992*

[a]Degrees of freedom ($n - 2$) = 58; *significant at 0.05; NS= not-significant.

4. Discussion

4.1. Effect of Elevated CO_2 on Gaseous Exchange Parameters

The results of this study showed down regulation of photosynthetic rate under elevated CO_2. But many previous studies reported that in many C3 species and terrestrial plants, increase leaf photosynthesis at elevated CO_2 due to enhancement of ribulosebiphosphate carboxylase/oxygenase (Rubisco) activity for carboxylation, but long-term exposure offsets this advantage by down-regulation of the process [20] [34] [58]-[60] and partly because the export of photosynthate from source to sink does not necessarily increase photosynthetic capacity. This reduction in photosynthetic capacity at high CO_2 attributed to lower concentration of Rubisco and more pronounced at low N supply [61] but reduction in Rubisco concentration is caused by accumulation of soluble carbohydrates is still a matter of debate [62]. Reference [63] argued that photosynthesis exceeds the capacity for carbohydrate export and utilization due to genetic limitations (such as determinate growth patterns) and environmental limitations (such as N deficiency or low temperature). Down-regulation of photosynthetic activity under CO_2 enrichment is caused by decreasing leaf N concentration, and reduced rate of transpiration owing to decreased stomatal conductance is partially responsible for poor N translocation as reported by [64] but photosynthesis acclimation ameliorated when N was added to growth medium adequately under elevated CO_2 [65]. This finding emphasizes the role of transpiration in acquisition of nitrogen (N) by leaves from the root environment and reveals existence of a feedback mechanism for photosynthetic acclimation at elevated CO_2. The findings also supports an explanation that decreased transpiration resulting from stomatal closure possibly limit plant N uptake by causing declines in mass flow of mobile N forms to the mycorrhizophere [66] However, the associated effects of reduced transpiration on leaf N concentration and its influence on Rubisco/photosynthetic activity are undetermined in the literature. Concentration of CO_2 is not a limiting factor for photosynthesis under N deficiency but CO_2 enrichment under such conditions down-regulates leaf photosynthesis [67]. References [58] [68] observed a positive correlation between low leaf N content and low photosynthesis at high CO_2 concentration. The results obtained in our study confirmed these findings where long-term exposure to high CO_2 increase specific leaf area and decrease leaf N concentration (**Figure 5**) resulting in decreased leaf photosynthesis, stomatal conductance and transpiration rate significantly. Our study also demonstrated that leaf N content was

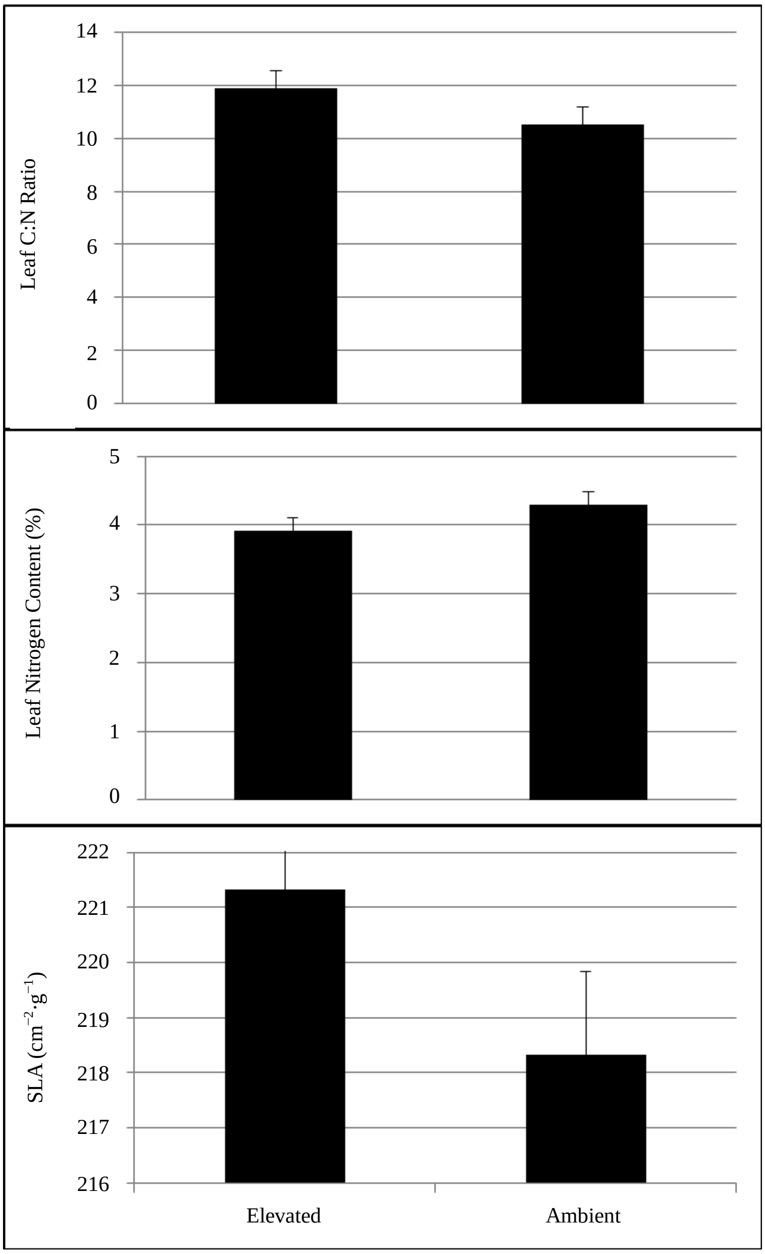

Figure 5. Specific leaf area (SLA), Leaf Nitrogen content and leaf C: N ratio of soybean under elevated & ambient (CO_2) at 44 DAP.

low by 5.7% (at 29 DAP) and 8.7% (at 44 DAP) under elevated CO_2 compared to ambient CO_2. A reduction in leaf N concentration with elevated CO_2 has been reported in different crop species [49] [61] [69] [70]. Our study suggests that the reduction in leaf N might be due to a greater increase in leaf area, as a result, the lack of proportionate gain in N by the plants (**Figure 5**). Increase in carbon (C) concentration and reduction in N content with increased C:N ratio due to elevated CO_2 has been reported in various investigations [65] [71]. Uptake of N may also be reduced at high CO_2 due to lower transpiration rate as reported by earlier studies [66] [72] [73].

On the contrary, many previous studies reported by [74] increased photosynthetic rates of soybean leaves with elevated CO_2 [75]-[80]. On the other hand, [81] reported that crop canopy photosynthetic rates can vary throughout the growing season mainly due to different requirements of photo-assimilates. However, [82] attributed this response to the typical characteristics of the soybean crop, which include: 1) high symbiotic N fixation capability; 2) the capacity to form an additional layer of palisade cells in the leaf tissue; 3) the capacity to shunt much of the photoassimilates into relatively inert starch rather than soluble sugars during photosynthesis; 4) a relatively strong leaf and stem sink during vegetative development; and 5) a strong seed sink during reproductive development. Plants that lack these capacities, either inherently or because of growth in limiting environments, are more likely to demonstrate some degree of down-regulation of photosynthesis [83]. Results of the other studies reported that four biochemical mechanisms for down-regulation of photosynthesis caused by source sink imbalance at elevated CO_2 are: 1) sugar repression of gene expression [84]; 2) insufficient N uptake [85]; 3) triose phosphate utilization rate limitation [86]; and 4) direct inhibition by saccharide content. On the other hand, the degree of down-regulation of photosynthesis was highly correlated with leaf glucose, fructose, and sucrose content and less correlated with starch content [87]. These differential responses could be related to growth conditions and nutrient stress. Our results agree with these results wherein no external fertilizers or nutrients were supplied to the plants during the study period and probably plants were under nutritional stress. The study on dry beans by [88] found that the net photosynthetic rate of plants grown in high nutrient levels did not show a down-regulation under elevated CO_2. This clearly suggests that acclimation response varies with the growth environment, age, nutrient status of the soil, and ability of plant roots to grow in an unrestricted volume.

The mechanism by which stomatal aperture responds to elevated CO_2 is mysterious [89] but the most important phenomena responsive/sensitive to increasing CO_2 levels is partial stomatal closure. In the present experiment, transpiration rate and leaf conductance was decrease under CO_2 enrichment. This agrees with the previous studies [6] [7] [24] [90]. A review on soybean showed that stomatal conductance was decreased by 31% at 450 - 550 $\mu mol \cdot mol^{-1}$ CO_2, 36% at 600 - 800 $\mu mol \cdot mol^{-1}$, and 51% at > 850 $\mu mol \cdot mol^{-1}$ of CO_2 with respect to ambient 330 - 360 $\mu mol \cdot mol^{-1}$ CO_2 [40] and 30% decrease in stomatal conductance with a doubling of CO_2 [8] [91]. In addition to decreased stomatal conductance, partial stomatal closure increases leaf resistance to transpiration water loss resulting in lower leaf transpiration rates. Reduction in transpiration was mainly attributed to decrease leaf conductance under elevated CO_2. This result, in agreement with the results of [92], concluded that although stomatal conductance may be decreased by about 40% for doubled CO_2, but water use by C3 crops under field conditions may probably be decreased only by up to 12%. If increases in leaf area due to doubled CO_2 are small, then the transpiration reductions would be meaningful, albeit small but on the contrary, if the increase in leaf area is too large, then no reductions in transpiration would be expected and even small increases might be possible. In our result, depletion of leaf N under elevated CO_2 could be attributed to reduced flow of the element in xylem owing to poor rate of transpiration due to partial closure of stomata at high CO_2. Nitrogen transfer from roots to leaves occurs in the xylem and the movement is mainly regulated by water flow derived from leaf transpiration.

Our experimental result demonstrated an increased WUE and intrinsic WUE under elevated CO_2 for soybean. However, WUE generally increases under high CO_2 in almost all previous experiments [6] [7] [10] [24]-[26]. In the present experiment, increased WUE under elevated CO_2 resulted from by increasing growth linked to prolonged photosynthetic activity more than increasing water consumption. This effect would be highly beneficial especially in water-limited rainfed areas where water conservation is necessary [93] [94]. In some studies, total canopy water use of soybean was reduced by CO_2 enrichment [95] [96], while in others it was unaffected [97] [98]. Numerous experiments have demonstrated that increased WUE is due to decreases in leaf transpiration rate [5] [11] [12] [15] [16] [18] [21].

4.2. Effect of Soil Moisture on Gas Exchange Parameters

Exposure of plants to water stress leads to decreases in photosynthetic rate, stomatal conductance, transpiration rate, and concomitant increase intercellular CO_2 in soybean. Stomatal closer reduces intercellular CO_2 concentration in leaves which imposes limitation on CO_2 assimilation, which causes an imbalance in photochemical activity at photosystem 2 (PS-2) and electron requirement for photosynthesis [99] [100]. Our results are also in conformity with the results of these studies. Except photosynthetic rate, all other parameters were not significant at both 42 and 47 DAP. Our experimental results indicated that plants under normal and high soil moisture levels, shows a significantly higher assimilation rate (7% to 16%) over plants under low soil moisture level. On the other hand, at all soil moisture levels photosynthetic rate was high (31.1%) at 47 DAP over 42 DAP. This high photosynthetic rate was attributed to favorable soil moisture conditions at 47 DAP compared to 42 DAP where gaseous exchange parameters measured at 24 h (47 DAP) and 72 h (42 DAP) of watering the soybean plants. Our study revealed that, high transpiration rate (18% to 26%) at high soil moisture compared to low and normal soil moisture level. On the other hand, 27.5% higher WUE at 72 h after watering (at 42 DAP) over 24 h after watering of plants. The plants showed adaptation mechanisms with progressive depletion of soil moisture by reducing stomatal conductance and transpiration rate. The favorable soil moisture content in soil increases the specific water content of soybean plants and shows an increase in trend with soil moisture availability from low to high (**Figure 6**) resulted in a positive impact on photosynthetic rate of plants. Our result, also in agreement with previous studies, where available soil water is necessary to maintain adequate photosynthetic rate during crop development and water deficit is known to decrease photosynthetic and transpiration rate [101]. Reduction of net photosynthesis in soybean plants can be induced by both stomatal and non-stomatal factors (of both biochemical and photochemical origin). On the other hand, [102] reported that decrease in photosynthetic rate under deficit soil moisture conditions may not necessarily be related to stomatal opening, but rather non-stomatal control of photosynthesis might have greater influence. In environments where there is water restriction caused by a lack of water from the soil or by a high atmospheric water demand, plants tend to close their stomata to conserve water via reducing transpiration losses and also reduces stomatal conductance (gs), which limits the entry of CO_2 into the substomatal chambers reducing the diffusion of C to the site of carboxylation, resulting in significant decreases in C assimilation [103]-[106]. Furthermore, [107] reports that the effects of water stress on the initial activity of Rubisco may be reproduced by induction of stomatal closure, independent of the reduction in the relative water content in the leaves of soybean plants. Thus, we can expect a lower regulation of photochemical and biochemical processes when the availability of CO_2 is the most limiting component for photosynthesis in plants under severe water stress [108]. The decrease in CO_2 diffusion from the atmosphere to the carboxylation site of Rubisco is generally considered to be the main cause of reduced photosynthesis under conditions of mild and moderate water deficits [106] [109]-[111]. The response of photosynthesis under water stress has been debated for decades, particularly with respect to what the most limiting factors for photosynthesis are [105] [112] [113]. However, there is still some controversy regarding the importance of the main physiological parameters and the time period over which they limit photosynthesis [106].

Soil-plant–atmospheric interactions will be altered by future climate change scenarios and leads to changes in the water balance and the amount of water available in the soil is crucial for crop yield. In warmer climates, increased evapotranspiration favors soil dryness and predicts that potential evaporation increases by about 2% - 3% for each 1˚C rise in temperature [114]. Thus, sites which are already at the limit with respect to water supply under current conditions are likely to be most sensitive to climate change, leading to an increase in the need for irrigation in dry areas, while more humid areas may be less affected [115].

4.3. Interaction Effect of CO_2 and Soil Moisture on Gaseous Exchange Parameters

Our results indicated that, an interactive effect of CO_2 and soil moisture levels was significant only on

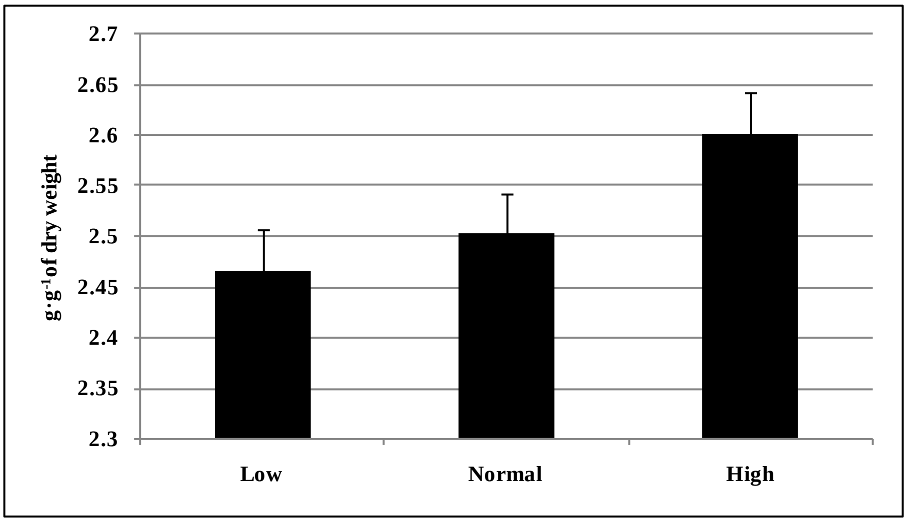

Figure 6. Specific water content of soybean (g of H_2O g^{-1} of dry weight) at 44 DAP under different soil moisture conditions (Low; Normal; and High).

photosynthetic rate at both 42 and 47 DAP of soybean. Photosynthetic rate was low when plants exposed to elevated CO_2 with favorable soil moisture conditions (normal & high) which was attributed to low leaf stomatal conductance and intercellular CO_2 concentration. Previous studies reported that stomatal closer reduces intercellular CO_2 concentration in leaves which imposes limitation on CO_2 assimilation, which causes an imbalance in photochemical activity at photosystem 2 (PS-2) and electron requirement for photosynthesis [99] [100]. This current study shows down regulation of photosynthetic rate under elevated CO_2 even with favorable soil moisture conditions. This down regulation of photosynthetic has been attributed to low leaf N concentration due to decline uptake of water from the N limited soil environment. Our results supports findings that leaf N content was low by 5.7% to 8.7% under elevated CO_2 compared to ambient CO_2. These results agree with many other studies [49] [61] [69] [70] who reported reduction in leaf N concentration with elevated CO_2 in many crop species.

The effects of elevated CO_2 on plants can vary depending on other interacting environmental factors including water, temperature, and available soil nutrients status. Elevated CO_2 makes C more available but plants equally need other resources in optimum to harvest benefit of raising atmospheric CO_2. Elevated CO_2 does not directly make these resources more available particularly uptake of water and nutrients. Uptake of nutrients, particularly N, was reduced at high CO_2 due to lower transpiration rate [66] [72] [73] coupled with a decrease in stomatal opening resulting in a low uptake of water, which increases soil moisture content. Therefore, the ability of plants to respond to elevated CO_2 with increased photosynthesis and growth may be limited under conditions of low mineral nutrients availability, particularly documented for N. In Free-Air Carbon Dioxide Exchange (FACE) experiments, there is less enhancement of photosynthesis by elevated CO_2 under low than high soil N conditions [116] [117]. Crop yield in FACE also appears to be enhanced by elevated CO_2 to a lesser extent under low-N than under high-N [116] [118] [119]. We suspect that improved growth of soybean under elevated CO_2 has further limited the available N in the present study where no external source of nutrients were supplied to the crop during the study period which reflected in low leaf N and high C:N ratio. The resultant inability of soybean plants to produce new sinks causes an imbalance in supply and demand which feedback on photosynthetic processes. This is supported by our leaf total N content (low by 5.7% at 29 DAP and 8.7% at 44 DAP) with more accumulation of carbohydrates resulting high C:N ratio. Our findings agree with those of [120], who concluded that photosynthetic acclimation results primary sink limitation in low N soils.

On the other hand, [121] reported that higher stomatal conductance in plants is known to increase CO_2 diffusion into leaves thereby favoring higher photosynthetic rates. Our result shows significant relations between photosynthetic rate and stomatal conductance ($r = +0.467^*$ at 42 DAP and $+0.643^*$ at 47 DAP) and similarly between stomatal conductance and intercellular CO_2 concentration ($r = +0.695^*$ at 42 DAP and $+0.816^*$ at 47 DAP). Due to favorable soil moisture condition at 47 DAP (24 h of watering) photosynthetic rate was relatively high both at ambient and elevated CO_2 over 72 h of watering (42 DAP). Further, our study revealed that low transpiration rate and C-i/CA ratio, high WUE, and A/gs ratio when plants were exposed to elevated CO_2 over ambient conditions. At 24 h and 72 h of watering (47 DAP), low transpiration rate and high WUE under elevated CO_2 over ambient CO_2, but increased transpiration rate and a reduction in WUE with increase in soil moisture levels from low to high. Under conditions of non-limiting soil water and elevated atmospheric CO_2, a reduction in stomatal conductance and decline in transpiration were observed in many herbaceous plants [7]. Decreases in stomatal conductance and transpiration rate of crops under elevated CO_2 in both irrigated and drought conditions has been reported by earlier studies [88] [93] [122]-[126].

This physiological behavior of crop plants under elevated CO_2 has greater implications, particularly in arid and semi-arid regions, where water is the most critical input [52] [53]. Two mechanisms are hypothesized to explain improved plant water relations under elevated CO_2. First, increases in plant photosynthetic rates in elevated CO_2 might lead to lower osmotic potential (OP) in leaf cells from higher concentrations of organic solutes, especially sugars of photosynthetic origin, which constitute a major fraction of osmotic substances in cells [127]. Thus, for a given water potential, lower values of OP should result in higher turgor potential and tissue water content. Second, since decreased gs in elevated CO_2 decreases leaf transpiration, it should also decrease the water potential gradient from soil to leaves. All these findings supporting the facts that for favorable crop growth under elevated CO_2 needs optimal resources particularly nutrients and soil moisture for positive feedback of crop plants but interactive effective of many resources with elevated CO_2 and environmental factors are inconclusive and greater dearth of literatures.

5. Conclusion

High CO_2 decreases photosynthetic rate, stomatal conductance, intercellular CO_2 concentration, relative intercellular CO_2 concentration, and transpiration rate. The down-regulation of photosynthesis is mainly caused by low leaf N content and high C:N ratio. This is supported with many other studies reported in the literature. Carbon dioxide enrichment increases leaf area causing low leaf N content and was found to increase C:N ratio and C content per unit mass of leaves resulting to lower protein content that will deteriorate the quality of grains may have feedback on nutritional security of future world. Water use efficiency enhanced under elevated CO_2 mainly through reduction in transpiration rate and water use by plants coupled with increased total dry matter production. In the present study, interactive effects of elevated CO_2 and soil moisture levels are significant but interactive effects of many resources with elevated CO_2 and environmental factors are inconclusive and greater dearth of literatures on this aspect. The effect of high CO_2 on plants depends on the availability of other resources, mainly nutrients and soil moisture. A positive feedback of crops from CO_2 enrichment will occur only when these resources are sufficient to meet crop demand.

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Declaration

Trade names and company names are included for the benefit of the reader and do not imply any endorsement or preferential treatment of the product by the authors or the USDA-ARS. USDA is an equal opportunity provider and employer.

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