

Habilitation Theses

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Physiology and Yield of Potential Alternative Crops and The Role of Plant Growth Regulators in Stress Tolerance

Crop Production and Horticultural Sciences



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1. Introduction

In Europe, increasing the area of legume crops has been identified as a key measure to transition towards more sustainable food systems (Schneider and Huyghe, 2015). Legumes are known to provide numerous agronomic benefits, including increased nitrogen availability in the soil, benefiting the subsequent crop, improved soil structure, and enhanced soil microbial activity (Jensen et al., 2010; Kopke and Nemecek, 2010). Legumes grown in crop rotation can enhance main crop yields, with larger benefits in low-input systems (Zhao et al., 2022). Protein crop yields in Europe are considered unstable (Pahl et al., 2006). The EU depends on imported high-protein plant products. The main reason for this is that protein crops in the EU are not competitive with the crops currently being produced. For example, soybean production has remarkably grown in the last four decades (Muller et al., 2021), however, to meet the expanding human population's need for plant protein, soybean production will have to increase by 70% over the next few years (Tilman et al., 2011), which seems unfeasible. European farmers are not motivated to cultivate these species on soils of good quality in appropriate environments, and that they prefer growing more profitable major crops in these environments (e.g., wheat, maize, and rapeseed) (Sellami et al., 2019). However, the competitiveness of crops can be expected to differ between regions within Europe because local conditions have a high influence on yield levels (Bues et al., 2013).

The rapid growth of the global population, combined with the escalating impacts of climate change, presents a formidable challenge to modern agriculture. Drought and salinity are among the most critical factors contributing to the decline in crop productivity and quality worldwide. According to the Food and Agriculture Organization (FAO), drought alone accounts for substantial yield losses in staple crops including wheat, maize, and rice, particularly in regions with high vulnerability to water scarcity (Boliko, 2019). Drought episodes are anticipated to become even more often and severe in many regions of the world, putting significant constraints on global agricultural supply (Zia et al. 2021). According to Wei et al. (2018), soybean yields can drop by more than half under drought conditions, resulting in significant losses for agricultural producers. At the same time, urbanization and industrial pressures are reducing the amount of arable land available, intensifying the urgency of developing drought-resilient agricultural systems while maintaining high nutritional and economic value. Such development strategies include improved varieties, shifts in recommended planting dates and rates, novel cropping sequences, and introduction of alternative or new crops. Sowing date is the most frequently varied option, which will surely be adjusted to increase temperature (White et al., 2011).

Chickpea is drought-tolerant and consequently may have an increasingly important role to play as climate change progresses and water becomes more limited in many places. In addition, it can be stored for a long time without a decline in its nutritional value, making it a major component in food and nutritional security (Ahmad et al., 2024). Chickpea, being traditionally sown in spring, can suffer from terminal drought and high temperatures during

reproductive stages, resulting in fewer pods and seeds, and reducing yields (Fang et al., 2010). Therefore, supplemental irrigation has been shown to significantly increase chickpea seed yield (Silva et al., 2014). Moreover, it has been observed that the date and density of sowing directly influence the growth and development, maturity time, and pod and seed production of chickpea, which affects its yield and quality (Husnain et al., 2015; Ali et al., 2018).

Mature chickpea grains contain 60–65% carbohydrates, 6% fat, and between 20 and 30% protein. Chickpea is also a good source of vitamins and minerals, including choline, folate, magnesium, potassium, and iron, and chickpeas are also high in vitamins A, E, and C (Yegrem et al., 2022).

Over the past two decades, quinoa (*Chenopodium quinoa* Willd.), a herbaceous pseudo-cereal plant native to the Andean region, has garnered global attention as a potential food security crop due to its high nutritional value and remarkable adaptability (Basantes-Morales et al. 2019). Its grains are rich in protein, essential fatty acids, minerals, vitamins, dietary fibers, and carbohydrates with hypoglycemic benefits while being gluten-free. The protein content in quinoa is notably higher than in cereals. Furthermore, quinoa demonstrates exceptional tolerance to cold, salt, and drought stress conditions, making it a resilient crop suitable for cultivation in diverse and marginal environments (Wali et al. 2022). Its genetic diversity enables quinoa to thrive across a broad range of environmental conditions, such as soil pH levels of 4.5 to alkaline, altitudes from sea level to over 4000 meters above sea level, temperatures ranging from -8°C to 38°C , and relative humidity levels of 40% to 100% (Jacobsen, 2003). Its physiological and biochemical mechanisms—including osmotic adjustment through proline and glycine betaine accumulation, efficient stomatal regulation, and robust antioxidant defense systems enable it to thrive under conditions where many traditional cereals fail (Ruiz-Carrasco et al., 2011). Quinoa has been successfully introduced and cultivated in several countries outside its center of origin, including Europe, where research initiatives have been undertaken to explore its adaptability and productivity (Poonia et al., 2024).

Nitrogen is a critical nutrient for plant growth and development, significantly influencing vegetative growth, yield, and metabolic processes (Montemurro and Diacono, 2016; Liu et al., 2022). Improving nitrogen use efficiency is vital to reduce environmental risks while maintaining agricultural productivity (Montemurro and Diacono, 2016). Nitrogen fertilizer has been shown to enhance quinoa's vegetative growth and grain yield. For example, Kansomjet et al. (2017) reported that nitrogen application rates of 94, 188, and 313 kg N ha^{-1} significantly increased the leaf area index (LAI), crop growth rate (CGR), and relative growth rate (RGR). Similarly, nitrogen rates of 80 and 120 kg N ha^{-1} improved quinoa grain yields to 3.1 and 3.5 kg ha^{-1} , respectively (Kaul et al., 2005).

To cope with stress conditions, plants undergo several changes on different levels, including reduced transpiration rate and stomatal conductance, decreased shoot growth and increased root growth, elevated osmolyte production (e.g., soluble sugars, proline, etc.) which

maintains cellular capacity of water retention through the osmolytes' anti-dehydration characteristic¹⁰. Proline can also protect the enzymatic system during drought occasions with its protective ability for several enzymes, in addition to its role in redox regulation¹¹. In order for these changes to happen, chemical signals are initiated in the root system, including elevated abscisic acid levels, leading to reactive oxygen species (ROS) production in higher levels. Low concentrations of ROS, however, were reported to potentially regulate the gene expression and the stress-responsive pathways, facilitate certain molecular and physiological alterations, cause a moderate accumulation of ROS which up-regulates the antioxidant system and, hence, partially alleviate the negative influence of several abiotic stresses, including drought^{16–20}. In Addition to hydrogen peroxide (H₂O₂), drought-induced effects were mitigated by foliar application of acetic acid (AA), as evidenced by improvements in soybean growth and leaf phenotypes, shoot height, shoot and root DW, total leaf area per trifoliate, and leaf succulence (Rahman et al. 2021); however, the potential different responses of soybean genotypes varying in drought tolerance are lacking. Moreover, the fluorescence traits in response to the sole and the mutual effect of drought and AA application are not fully studied either.

2. Selection of Topic

Despite their agronomical, environmental, and nutritional benefits, the production area of grain legumes remains low in Europe. In 2020, they represented less than 4% of European cropland, in contrast to 14.9% worldwide (FAOSTAT, 2023). Indeed, grain legume yields are often considered to be more variable than cereal yields, especially as they are frequently sown in spring, which makes them more exposed to heat stress and water deficit during key stages of their growing cycle (Falconnier et al., 2020). Drought can strongly affect grain legume growth, reproduction, and yield (Basal, 2021). Climate change is likely to increase the occurrence of such stresses, and thus impact grain legume performances (Ahmed et al., 2022).

Chickpea is cultivated on large scale in arid and semiarid environment (Mohammed et al., 2017). About 90% of the world's chickpea is grown under rainfed conditions where the crop grows and matures on a progressively depleting soil moisture profile and experiences terminal drought, a condition in which grain yield of chickpea is low. Average chickpea yield remains low in the major chickpea producing countries mainly due to inadequate water supply (Soltani and Sinclair, 2012). That said, selected alternative sowing dates other than the traditional, sowing dates, in addition to exploring the potentials of supplemental irrigation benefits in stabilizing chickpea yield and quality are of vital importance, especially in regions where chickpea is not grown widely.

On the other hand, and despite its potential, quinoa is not yet cultivated in Hungary. Considering Hungary's diverse and suitable agroecological conditions, introducing and cultivating quinoa could play a crucial role in ensuring food and nutritional security. However, there is a lack of experimental data regarding the effects of nitrogen application rates on the physiology, growth, yield, and seed quality of quinoa under various soil conditions in the region.

In addition, although the positive effects of exogenous application of ROS (e.g., H₂O₂ and AA) at different concentrations on several plant species are well documented, most of these

studies focused on the seedlings of these species (e.g. 1.5 mM H₂O₂ on cucumber seedlings (Sun et al., 2016), 0.5 mM H₂O₂ on tomato plants (Khan et al., 2018), 1 mM H₂O₂ on soybean (Ishibashi et al., 2011), 10 mM H₂O₂ on maize seedlings (Terzi et al., 2014) or on the pre-treatment with H₂O₂ (e.g. Liu et al. (2010) on cucumber) rather than later developmental stages. Moreover, whether exogenous H₂O₂ spray can help the recovering plants after drought is finished and/or plants that are suffering from continuous drought is not well documented. It would therefore be of vital importance to address these questions properly. This research directly addresses the urgent need for crops that can maintain productivity under abiotic stress conditions while contributing to long-term soil health. By elucidating the physiological and biochemical mechanisms through which PGRs enhance crop's resilience, and by evaluating its agronomic value in crop rotation systems, this research seeks to generate knowledge that is highly relevant for both plant science and agricultural practice. The expected outcomes have the potential to enhance crop breeding strategies, sustainable soil management practices, and policy frameworks aimed at achieving climate-resilient agriculture.

That said, the aims of this research are to:

- 1) evaluate the morpho-physiology, yield components, and seed quality of different chickpea varieties in response to late sowing date, and the possibility of engaging chickpea in a cereal-legume crop rotation through a sustainable, all-year-long crop rotation.
- 2) Understand whether supplemental irrigation will be necessary to guarantee profitable chickpea yield and its possible effects on the seed quality.
- 3) evaluate the physiological, growth, yield, and seed quality responses of different quinoa cultivars to nitrogen fertilization in Debrecen, Hungary.
- 4) evaluate the response of soybean to temporal and continuous drought stress
- 5) test the hypothesis that low concentrations of PGRs will have positive influence on the morpho-physiology and the biochemistry of soybean plants that suffer from drought stress during different growth stages.

3. Materials and Methods

3.1. Field Experiments

Two field experiments were conducted at the experimental garden of the Faculty of Agricultural and Food Sciences and Environmental Management of the University of Debrecen in 2024 and 2025. The soil type is chernozem soil. Data of daily precipitation, high and low temperatures, and relative humidity were collected from the meteorological station on the experimental site (Precision Crop Research and Development Service Center).

3.1.1. The Effects of Sowing Date on The Morpho-physiology, Yield Components, and Seed Quality of Chickpea under Supplemental Irrigation Conditions

Three chickpea varieties (Amorgos, Elmo, and Orion) were sown at three different sowing dates: the first sowing date (SD1) was on 2 May in 2024 and on 1 May in 2025, the second sowing date (SD2) was on 3 June in 2024 and on 1 June in 2025, and the third sowing date (SD3) was on 1 July in both 2024 and 2025. Half of the plots of each sowing date were supplementally irrigated when needed to keep the field capacity (FC%) at 65-70% FC using the method described by Gebeyhu et al. (2024), whereas the other half was left under rainfed conditions. The experiment was laid out in a randomized complete block design (RCBD) with

4 replicates. The dimensions of each plot were 3 * 2 m. Distance among rows within each plot was 15 cm. The plant density was 49 plants/m².

3.1.2. The Effects of Nitrogen Application and Rates on The Physiology and Yield of Quinoa under Supplemental Irrigation Conditions

Two quinoa varieties (Titicaca and Vikinga) were sown on 2 May in 2024 and on 1 May in 2025. Three nitrogen fertilization rates; 0 kg N/ha (N1), 75 kg N/ha (N2), and 150 kg N/ha (N3) were applied one week after sowing. Half of the plots of each fertilization rate were supplementally irrigated when needed to keep the field capacity (FC%) at 65-70% FC using the method described by Gebeyhu et al. (2024), whereas the other half was left under rainfed conditions. The experiment was laid out in a randomized complete block design (RCBD) with 4 replicates. The dimensions of each plot were 3 * 2 m. Distance among rows within each plot was 10 cm. The plant density was 330 plants/m².

3.1.3. Statistical Analyses

GenStat 20th edition (VSN International Ltd, UK) software was used to run analysis of variance (3-way ANOVA) test to indicate statistical significance at 5% level ($p \leq 0.05$), followed by Duncan's multiple range test (DMRT) to indicate the statistically significant treatments. All data provided are the means of 8 biological replicates $\pm$ standard error (SE).

3.2. Controlled Environment Experiments

Two experiments were conducted in a hydroponic system at the controlled-climate chamber of the Institute of Applied Plant Biology of the University of Debrecen in 2022.

3.2.1. The Effects of Exogenous Application of Hydrogen Peroxide on The Morpho-physiology and Biochemistry of Soybean under Severe Drought Stress Conditions

Two soybean varieties; Coraline (drought-susceptible) and Speeda (drought-tolerant) were chosen for this study. Severe drought stress was applied using polyethylene glycol (PEG 6000) (VWR International bvba Geldenaaksebaan, Leuven, Belgium) at a concentration of 10% (w/v) dissolved properly and completely in the nutrient solution of each pot (except control treatment). Drought stress was applied starting from R1 stage, and then either lifted at the end of R2 stage or kept in place afterwards. Three hydrogen peroxide (H₂O₂) concentrations; 1, 5 and 10 mM were exogenously sprayed every other day throughout the flowering stage, and a control treatment was alternatively sprayed with distilled water (DW). At the end of the flowering stage, the pots of each variety were further divided into two groups; the first group was allowed to recover from drought stress by terminating PEG application, whereas the second group was kept under continuous drought stress conditions. Thus, there was 9 treatments for each variety; 4 treatments sprayed with either 0, 1, 5 or 10 mM H₂O₂ (D, D1, D5 and D10, respectively) under drought stress imposed between R1 and R2 stages, 4 treatments sprayed with either 0, 1, 5 or 10 mM H₂O₂ (CD, CD1, CD5 and CD10, respectively) under continuous drought stress imposed from R1 stage onwards, in addition to a control treatment, where the plants were kept under optimum conditions and were sprayed with DW whenever the other treatments were sprayed with any concentration of H₂O₂.

To monitor the response of the different treatments, sampling for the different traits was made at 3 different occasions; 3 days after drought stress application (3 days after the beginning of R1 stage, equivalent to 51 and 59 days after sowing (DAS) in Coraline and Speeda, respectively), 3 days after terminating the drought stress as mentioned earlier (3 days after the ending of R2 stage and the beginning of R3 stage, equivalent to 64 and 73 DAS in Coraline and Speeda, respectively) and at the end of the experiment (at the end of R4 stage, equivalent to 89 and 101 DAS in Coraline and Speeda, respectively). At each sampling occasion, the second-most developed leaf was selected. The experiment was laid out in a randomized complete block design with 3 replicates, so the final pot number was 54 (2 varieties * 9 treatments * 3 replicates).

Seeds of both varieties were surface sterilized using 6 % (v/v) H₂O₂ for 20 min, rinsed extensively with deionized water and germinated geotropically between moisten filter papers at 22 °C. After germination, 10 homogenous seedlings with good vigor were transferred into 3-liter pots, and the number of seedlings was reduced later to 7 homogenous seedlings per pot. Each pot received 300 ml of Hoagland solution, in addition to corresponding PEG solution. The nutrient solution was renewed every 3 days.

During the whole experimental period, the day/night temperature was kept at 26/19 °C with 65% relative humidity and light intensity of 300 $\mu\text{mol m}^{-2} \text{s}^{-1}$ during the light period.

3.2.2. The Effects of Exogenous Application of Acetic Acid on The Morphophysiology of Soybean under Severe Drought Stress Applied at Early Stages

The seeds of two soybean varieties, 'Speeda' and 'Coraline', were surface sterilized, rinsed well with deionized water, and geotropically germinated within moist filter sheets similar to the experimental procedure explained in 3.2.1 section. Seedlings with good vigor were potted in 1.7 L pots after germination. Three seedlings were placed in each pot. Each pot received 170 ml of Hoagland solution. Every three days, the nutrient solution in each pot was replaced with a fresh one. Drought was induced using PEG 6000 (VWR International bvba Geldenaaksebaan, Leuven, Belgium) when the plants reached the V3 stage (BBCH 103) and kept for 8 days. The PEG concentrations were 0% (D0=control) and 10% (D1=drought-stress treatment). Along with 10% PEG treatment, 2 ml of 20 mM Acetic Acid (AA) was sprayed on drought-stressed plants each time the nutrient solution was changed, starting from the day PEG was applied until the end of the experiment (8 days after drought stress application) (i.e., at days 1,4 and 7 of PEG imposition). The experiment was laid out in a randomized complete plot design with 3 replicates. Thus, there were 3 treatments: control treatment (D0), growing in ideal conditions with no drought stress; drought-stressed treatment (D1) and drought-stressed treatment with acetic acid spray applied (D2). The total number of pots was 18 (2 varieties * 3 treatments * 3 replications).

3.2.3. Statistical Analyses

GenStat 20th edition (VSN International Ltd, UK) software was used to run analysis of variance (3-way ANOVA) test to indicate statistical significance at 5% level ($p \leq 0.05$), followed by Duncan's multiple range test (DMRT) to indicate the statistically significant treatments. All data provided are the means of 3 biological replicates $\pm$ standard error (SE).

4. Results and Discussion

4.1. Field Experiments

4.1.1. The Effects of Sowing Date on The Morpho-physiology, Yield Components, and Seed Quality of Chickpea under Supplemental Irrigation Conditions

Leaf Area Index (LAI)

Regardless of irrigation scheme, the leaf area index (LAI) was significantly lower in all varieties sown at late sowing date (SD3) as compared to spring sowing date (SD1). Irrigation enhanced LAI of all varieties, with more pronounced increments in Amorgos and Elmo varieties at SD1 and SD2. Under both irrigation regimes, Elmo plants had significantly higher LAI at all sowing dates, whereas Amorgos had the lowest LAI (Figure 1).

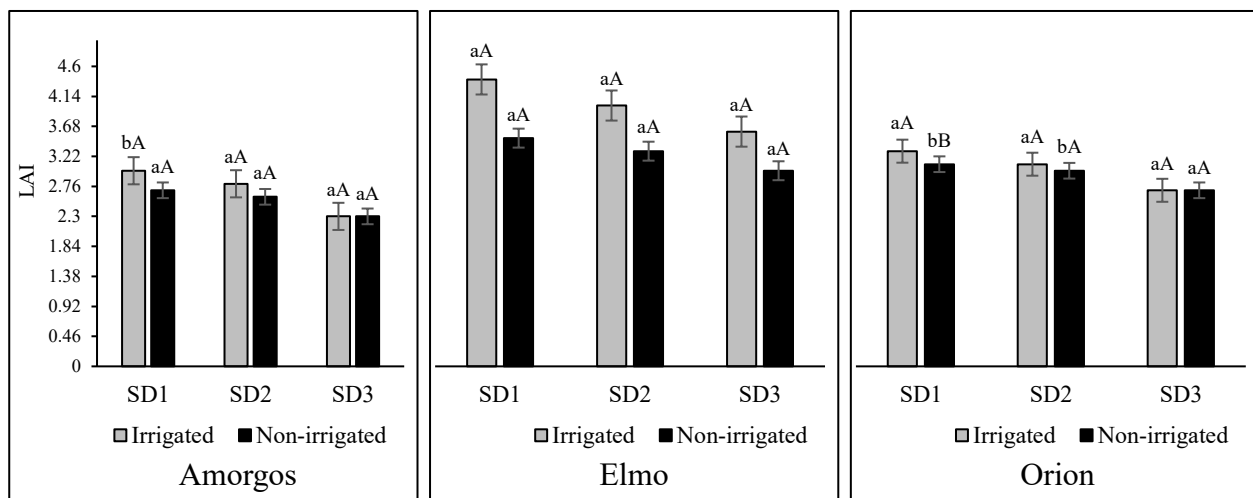


Figure 1. Leaf Area Index (LAI) of three chickpea varieties (Amorgos, Elmo, and Orion) sown at three different sowing dates (SD1, SD2, and SD3) under supplemental irrigation (irrigated) and rainfed (non-irrigated) conditions. $n = 8$, $\pm$ SD. Different small letters indicate significant differences ($p \leq 0.05$) among sowing dates within each irrigation scheme. Different capital letters indicate significant differences ($p \leq 0.05$) between the irrigated schemes within each sowing date.

Normalized Difference Vegetation Index (NDVI)

Under both irrigation regimes, the NDVI decreased significantly at the late sowing date (SD3) of Amorgos variety, whereas no significant differences were observed in the other two varieties. The irrigation effect was valid in all varieties sown in spring (SD1), where the irrigated plants had significantly higher NDVI values. However, that effect was not present at SD2 and SD3. Regardless of irrigation scheme, Elmo had the highest NDVI, with more pronounced differences in spring (SD1) and late (SD3) sowing dates (Figure 2).

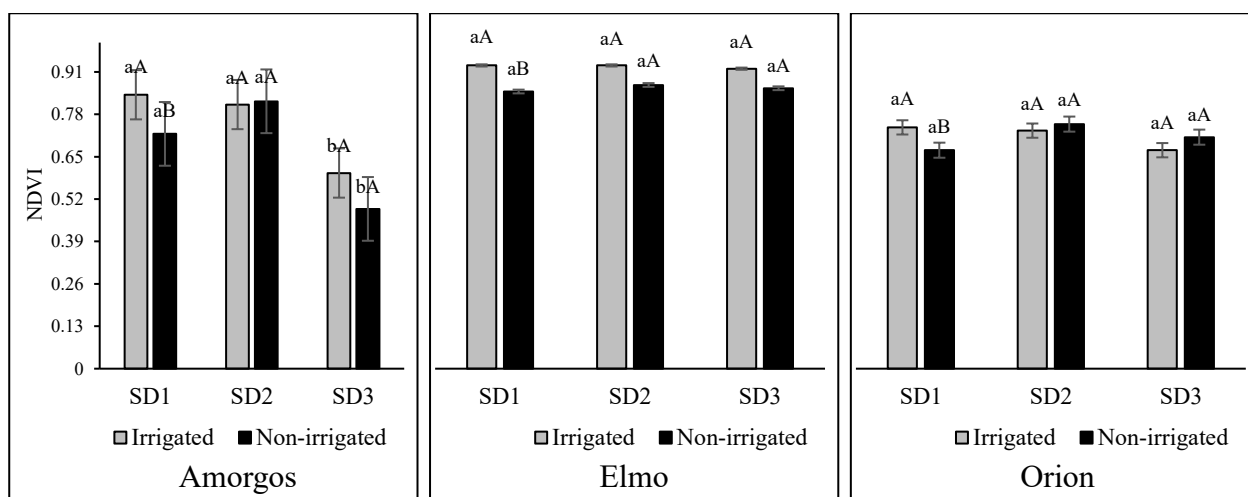


Figure 2. Normalized Difference Vegetation Index (NDVI) of three chickpea varieties (Amorgos, Elmo, and Orion) sown at three different sowing dates (SD1, SD2, and SD3) under supplemental irrigation (irrigated) and rainfed (non-irrigated) conditions. $n = 8, \pm SD$. Different small letters indicate significant differences ($p \leq 0.05$) among sowing dates within each irrigation scheme. Different capital letters indicate significant differences ($p \leq 0.05$) between the irrigated schemes within each sowing date.

Plant Height

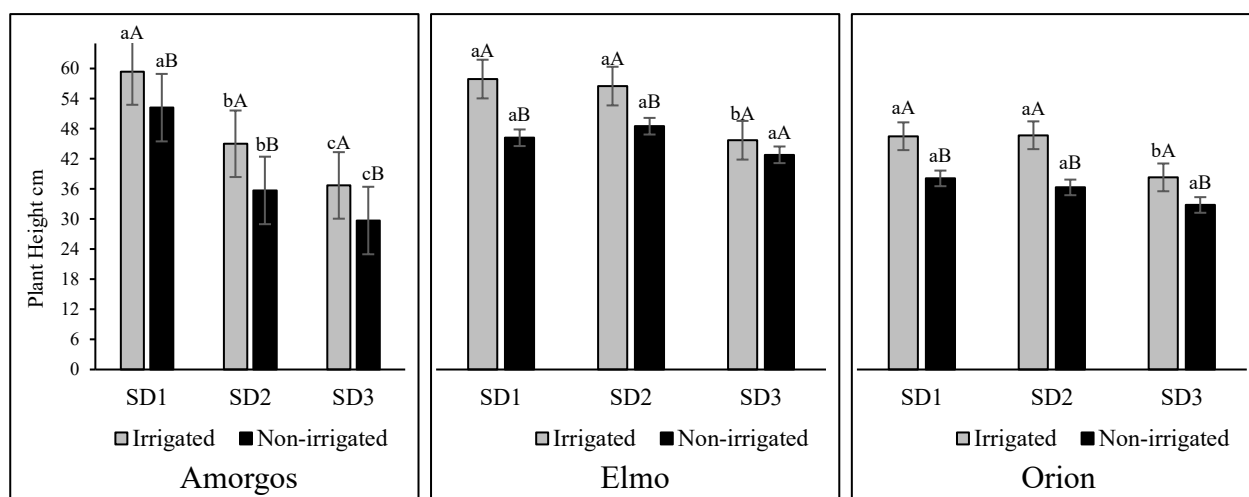


Figure 3. Plant height (cm) of three chickpea varieties (Amorgos, Elmo, and Orion) sown at three different sowing dates (SD1, SD2, and SD3) under supplemental irrigation (irrigated) and rainfed (non-irrigated) conditions. $n = 8, \pm SD$. Different small letters indicate significant differences ($p \leq 0.05$) among sowing dates within each irrigation scheme. Different capital letters indicate significant differences ($p \leq 0.05$) between the irrigated schemes within each sowing date.

Under irrigated conditions, the plant height was significantly higher in all varieties for plants sown in spring (SD1) as compared to those sown late (SD3). When irrigation was not applied, however, the difference was observed only in Amorgos. Irrigation had a major effect on this trait, as the irrigated plants of all varieties were significantly taller than their non-irrigated counterparts at all sowing dates, except for Elmo plants at late (SD3) sowing date, where the difference was not significant. El-Waraky and Koliey (2000) found that irrigation at branching, flowering and pod development stages resulted in elevated plant height. Elmo plants were significantly taller than Orion plants under both irrigation regimes at all sowing

dates. Moreover, Elmo plants were significantly taller than those of Amorgos at both SD2 and SD3, but not at SD1 (Figure 3).

Total Carotenoid Content

No significant differences were observed in the total carotenoid content of either of the varieties among sowing dates. Under the non-irrigated scheme, however, the varieties showed different responses, where the total carotenoid content increased significantly in Elmo, but decreased significantly in Orion at the late (SD3) sowing date. The total carotenoid content of all varieties was higher under non-irrigated, compared to irrigated scheme, but the differences were significant only in Elmo at SD3 and in Orion at SD1 and SD2. Amorgos, on the other hand, did not show any measurable differences in this trait. No measurable differences in this trait were observed among the three varieties at any sowing date under irrigated scheme. However, Orion had significantly higher total carotenoid content than Elmo at spring (SD1), but not at late (SD3) sowing date (Figure 4).

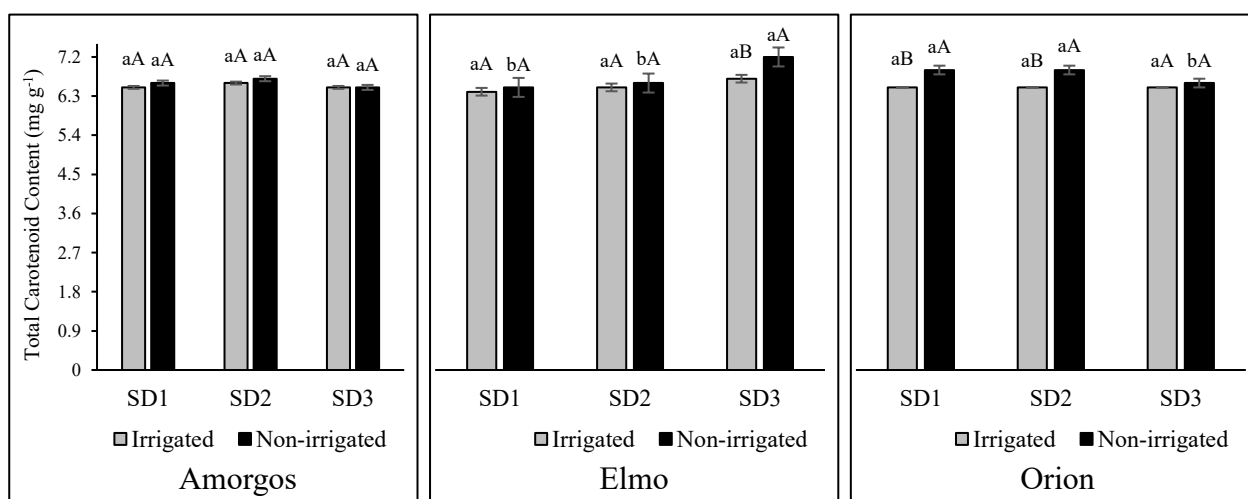


Figure 4. Total carotenoid content (mg g^{-1}) of three chickpea varieties (Amorgos, Elmo, and Orion) sown at three different sowing dates (SD1, SD2, and SD3) under supplemental irrigation (irrigated) and rainfed (non-irrigated) conditions. $n = 8$, $\pm\text{SD}$. Different small letters indicate significant differences ($p \leq 0.05$) among sowing dates within each irrigation scheme. Different capital letters indicate significant differences ($p \leq 0.05$) between the irrigated schemes within each sowing date.

Total Chlorophyll Content

There were no significant differences among the sowing dates in the total chlorophyll content of the plants of the studied varieties under both irrigation schemes, with one exception in Elmo variety under the non-irrigated scheme. Moreover, Irrigation did not have any measurable effect on any variety at all sowing dates. Elmo plants had significantly higher total chlorophyll content than the other two varieties under both irrigation schemes at all sowing dates, with one exception, where all three varieties had similar values of this trait at the late (SD3) sowing date under non-irrigated scheme (Figure 5).

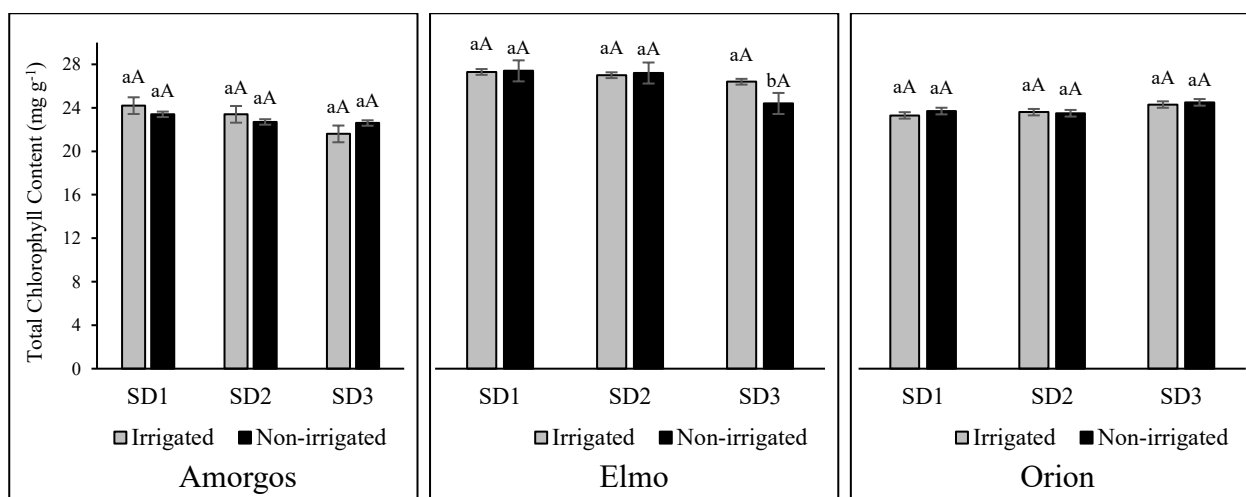


Figure 5. Total chlorophyll content (mg g^{-1}) of three chickpea varieties (Amorgos, Elmo, and Orion) sown at three different sowing dates (SD1, SD2, and SD3) under supplemental irrigation (irrigated) and rainfed (non-irrigated) conditions. $n = 8$, $\pm\text{SD}$. Different small letters indicate significant differences ($p \leq 0.05$) among sowing dates within each irrigation scheme. Different capital letters indicate significant differences ($p \leq 0.05$) between the irrigated schemes within each sowing date.

Days to Flowering

Under both irrigation schemes, the number of days to flowering decreased significantly in all three varieties sown late (SD3) compared to their counterparts sown in spring (SD1). Irrigation also had a major effect on this trait, since the days to flowering of the non-irrigated plants of all varieties at all sowing dates (except for Amorgos at SD3 and Orion at SD1) were significantly less compared to their irrigated counterparts. It was previously reported that the decrease in days to flowering and maturity can be measurably attributed to the increase in temperature since high temperature can shorten crop life cycle by speeding up the crop growth and development stages (Mohammed et al., 2017). Earlier, Anwar et al. (2003) concluded that temperature was the dominant factor that affected Kabuli chickpea phenology sown at different sowing dates and under different irrigation schemes. The authors reported that the late-sown chickpea encounters higher temperatures that enhanced phenological development, shortening the period from sowing to flowering and the start of pod filling. They also reported that comparisons between the rainfed and irrigated treatments indicated that drought stress could induce substantial reductions in the duration to flowering and crop maturity in Kabuli chickpea (Anwar et al., 2003). The number of days to flowering of Orion plants was significantly higher than those of the other varieties under both irrigation schemes at all sowing dates, except for the irrigated varieties at the spring (SD1) sowing dates, where the differences of this trait among the three varieties were very small (Figure 6).

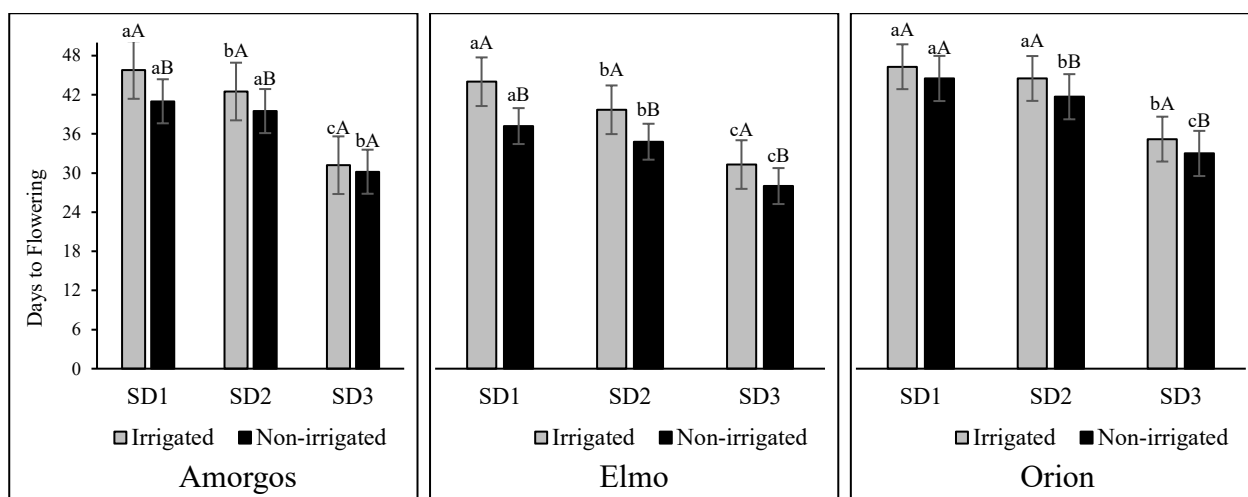


Figure 6. Days to flowering of three chickpea varieties (Amorgos, Elmo, and Orion) sown at three different sowing dates (SD1, SD2, and SD3) under supplemental irrigation (irrigated) and rainfed (non-irrigated) conditions. $n = 8$, $\pm$ SD. Different small letters indicate significant differences ($p \leq 0.05$) among sowing dates within each irrigation scheme. Different capital letters indicate significant differences ($p \leq 0.05$) between the irrigated schemes within each sowing date.

Flower Number per Plant

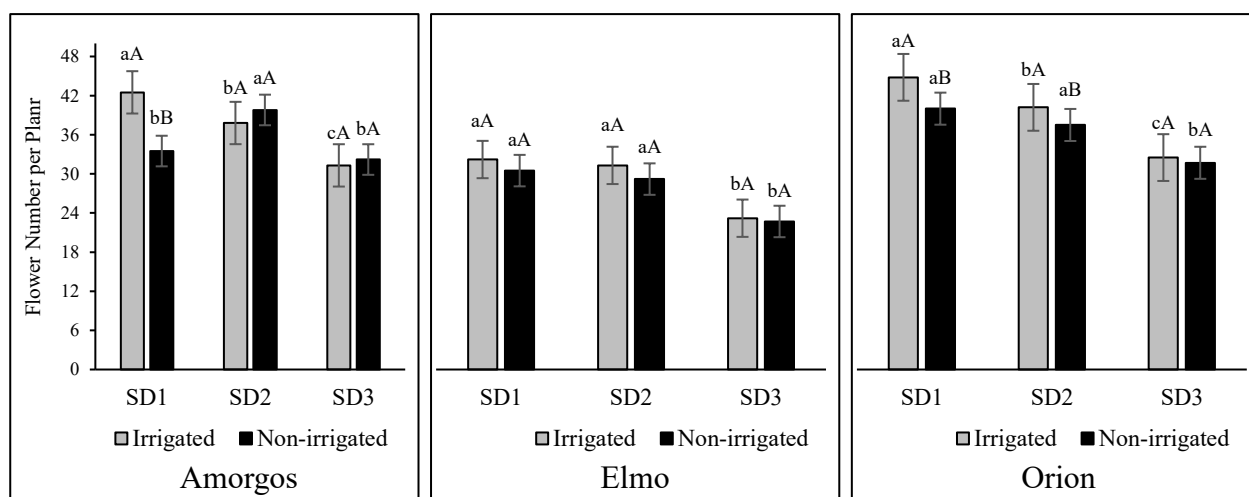


Figure 7. Flower number per plant of three chickpea varieties (Amorgos, Elmo, and Orion) sown at three different sowing dates (SD1, SD2, and SD3) under supplemental irrigation (irrigated) and rainfed (non-irrigated) conditions. $n = 8$, $\pm$ SD. Different small letters indicate significant differences ($p \leq 0.05$) among sowing dates within each irrigation scheme. Different capital letters indicate significant differences ($p \leq 0.05$) between the irrigated schemes within each sowing date.

The flower number per plant of all studied varieties was significantly lower at the late (SD3) sowing date than that of spring (SD1) sowing date under both irrigation schemes (except for the case of Amorgos under non-irrigated scheme, where the difference was insignificant). According to Jumrani and Bhatia (2014), high temperatures during flowering often decrease flower number of chickpeas. The studied varieties responded differently to irrigation; Elmo had relatively similar number of flowers per plant under both irrigation regimes at all sowing dates. Amorgos plants had significantly higher number of flowers per plant under irrigated scheme at SD1 only, whereas Orion plants had so at SD1 and SD2, but not at SD3. At all

sowing dates, Orion had significantly higher number of flowers per plant than Elmo, regardless of irrigation scheme, in addition to having significantly higher values of this trait than Amorgos at all sowing dates under irrigated scheme and at SD1 under non-irrigated scheme (Figure 7).

Pod Number per Plant

Under both irrigation schemes, there were no significant differences in the number of pods per plant among the sowing dates in all three varieties. Similar conclusion was reported earlier by Munirathnam and Sangita (2009), who concluded that the dates of sowing did not influence number of pods per plant or seed yield. Moreover, the number of Amorgos did not record any measurable differences in response to irrigation at any sowing date, whereas Orion and Elmo plants had significantly higher number of pods per plant under irrigated scheme at all sowing dates. Bakhsh et al. (2007) reported that 48% increase in number of pods per plant on average basis was recorded due to irrigation. Nawab et al. (2013) reported that increased water availability resulted in increased pod number per plant, in addition to the biomass and the seed yield, justifying that conclusion by the available water being enough during the reproductive stages at the experimental site. At all sowing dates, Orion plants had significantly higher number of pods per plant as compared to the other varieties under irrigated scheme, whereas it was higher than that of Elmo under non-irrigated scheme (Figure 8).

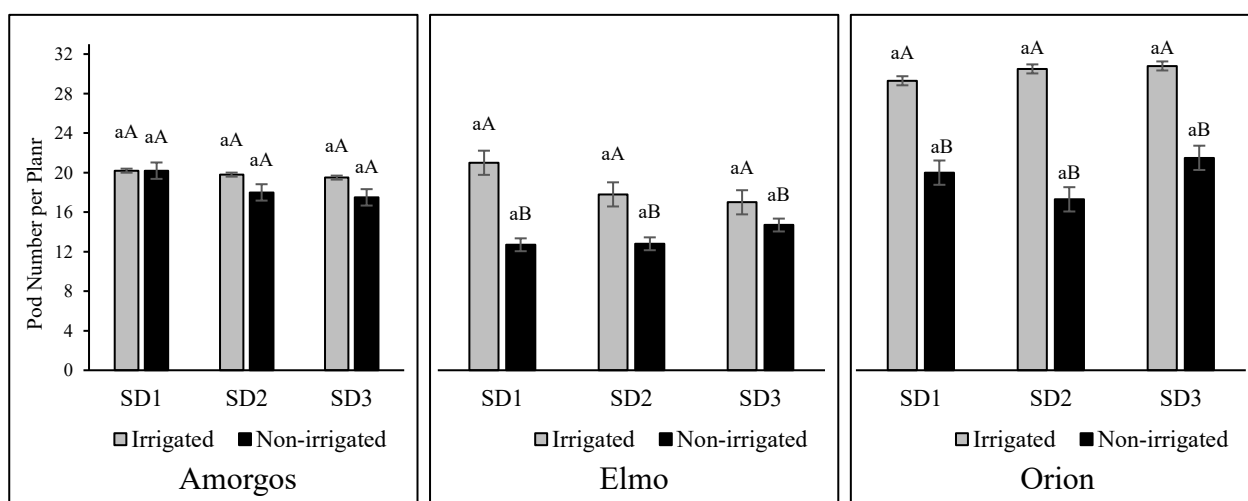


Figure 8. Pod number per plant of three chickpea varieties (Amorgos, Elmo, and Orion) sown at three different sowing dates (SD1, SD2, and SD3) under supplemental irrigation (irrigated) and rainfed (non-irrigated) conditions. $n = 8$, $\pm$ SD. Different small letters indicate significant differences ($p \leq 0.05$) among sowing dates within each irrigation scheme. Different capital letters indicate significant differences ($p \leq 0.05$) between the irrigated schemes within each sowing date.

Seed Number per Plant

Under irrigated scheme, Orion had significantly lower seed numbers per plant than Amorgos at all sowing dates, whereas there were no measurable differences in this trait among the studied varieties under non-irrigated scheme, regardless of sowing date. Irrigation had differential effects on the studied varieties; it did not have any significant effect on Amorgos plants, regardless of sowing date, whereas it significantly increased this trait in Elmo plants

at SD1 and in Orion plants at both SD1 and SD2, but not at SD3. At all sowing dates and under both irrigation schemes, the number of seeds of Orion was significantly higher than that of the other varieties, whereas Elmo had the lowest number of seeds per plant (Figure 9).

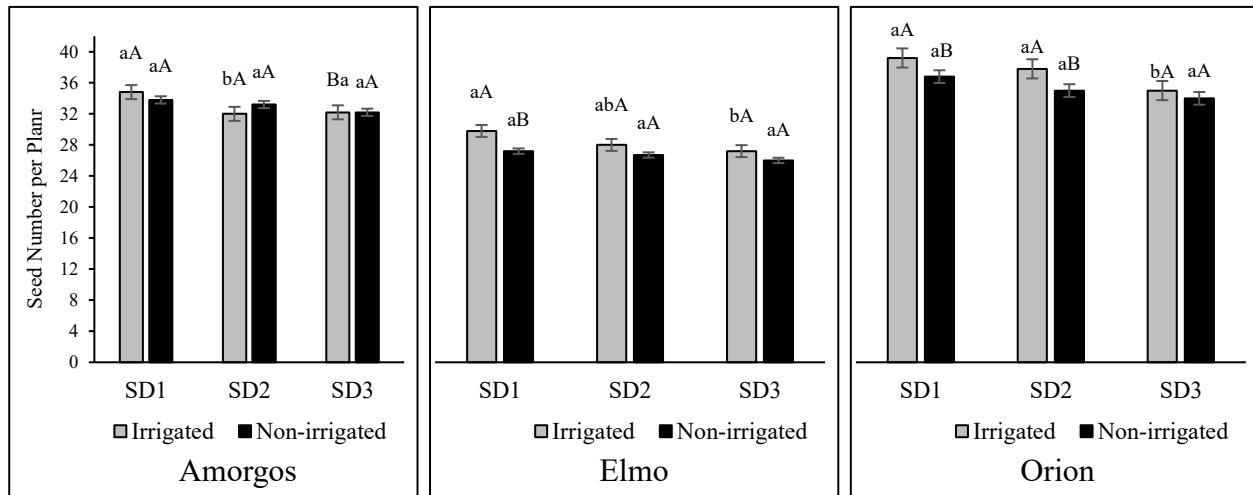


Figure 9. Seed number per plant of three chickpea varieties (Amorgos, Elmo, and Orion) sown at three different sowing dates (SD1, SD2, and SD3) under supplemental irrigation (irrigated) and rainfed (non-irrigated) conditions. $n = 8$, $\pm$ SD. Different small letters indicate significant differences ($p \leq 0.05$) among sowing dates within each irrigation scheme. Different capital letters indicate significant differences ($p \leq 0.05$) between the irrigated schemes within each sowing date.

100-seed Weight

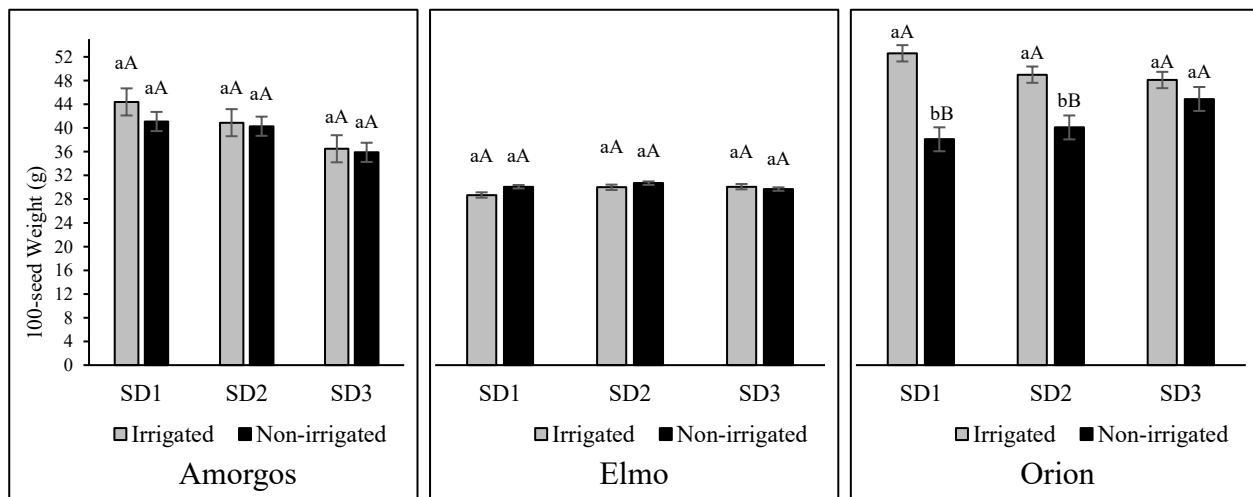


Figure 10. 100-seed weight (g) of three chickpea varieties (Amorgos, Elmo, and Orion) sown at three different sowing dates (SD1, SD2, and SD3) under supplemental irrigation (irrigated) and rainfed (non-irrigated) conditions. $n = 8$, $\pm$ SD. Different small letters indicate significant differences ($p \leq 0.05$) among sowing dates within each irrigation scheme. Different capital letters indicate significant differences ($p \leq 0.05$) between the irrigated schemes within each sowing date.

Under irrigated scheme, the sowing date had no influence on the 100-seed weight of any variety. Under non-irrigated scheme, however, the 100-seed weight of Orion plants sown late (SD3) was significantly higher than that of the plants sown earlier (SD1 and SD2), whereas the sowing date of both Amorgos and Elmo did not affect this trait measurably. Moreover, the 100-seed weight of both Amorgos and Elmo varieties was not affected by irrigation,

whereas it was significantly higher for Orion plants at SD1 and SD2 under irrigated scheme, but not at SD3. The 100-seed weight of Orion was significantly higher than that of Elmo at all sowing dates and under both irrigation schemes. Moreover, Orion had significantly higher 100-seed weight than Amorgos did at all sowing dates under irrigated scheme and at SD3 under non-irrigated scheme (Figure 10).

Seed Yield

The seed yield of Elmo was significantly lower at the late (SD3) sowing date than that at the other (SD1 and SD2) sowing dates, regardless of irrigation scheme. In Amorgos, this trait did not show any significant effect among the sowing dates under both irrigation schemes. In Orion, the sowing date did not have an effect under irrigated scheme, but did under non-irrigated scheme, where the late (SD3) sowing date decreased the seed yield significantly. The irrigated plants of all studied varieties resulted in significantly higher seed yield at all sowing dates compared to their non-irrigated counterparts. It was previously reported that supplemental irrigation at flowering and podding stages increased the seed yield of chickpea sown late in the season (Amiri et al., 2016). In addition, the results of a study by Mohammed et al. (2017) also showed that better responses from supplemental irrigation could be obtained when irrigation water was applied at the critical time of the crop growth stages (flowering, grain and pod setting).

At all sowing dates and under both irrigation schemes, Orion resulted in the highest seed yield, followed by Amorgos, whereas Elmo's seed yield was the lowest. In a study that evaluated 24 chickpea varieties (including Orion) at 4 locations in North America, the authors indicated the presence of significant variability among chickpea varieties (Ahmad et al., 2024), which agreed with earlier findings by Zhang et al. (2021) and Yegrem et al. (2022), who evaluated different chickpea varieties and genotypes at different locations and found significant differences in the yield among the genotypes and the locations. The authors justified their findings by genetic variability in the varieties/genotypes and the climatic condition (Figure 11).

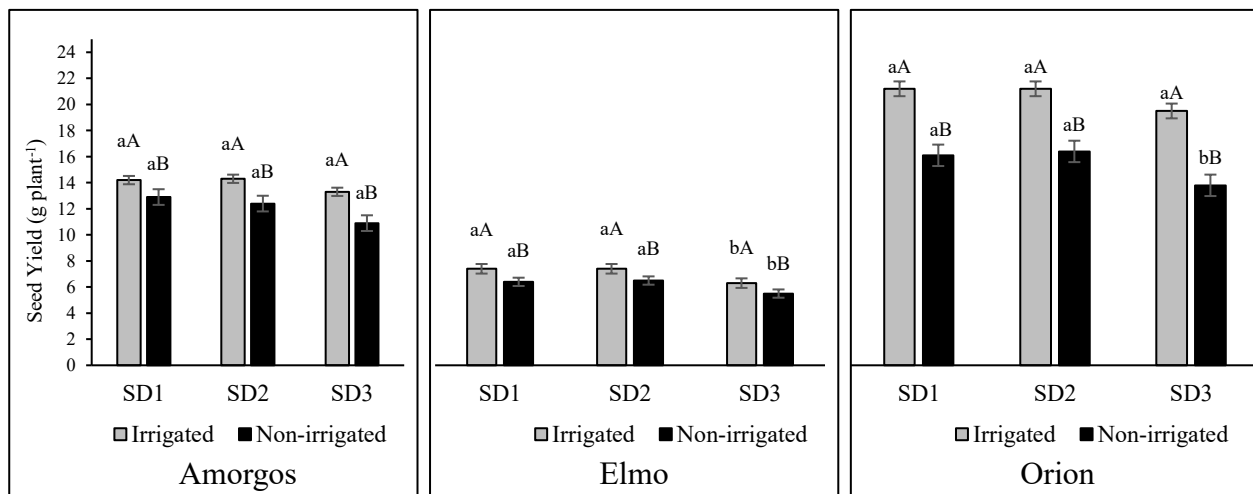


Figure 11. Seed yield (g plant⁻¹) of three chickpea varieties (Amorgos, Elmo, and Orion) sown at three different sowing dates (SD1, SD2, and SD3) under supplemental irrigation (irrigated) and rainfed (non-irrigated) conditions. n = 8, $\pm$ SD. Different small letters indicate significant differences ($p \leq 0.05$) among sowing dates within each irrigation scheme. Different capital letters indicate significant differences ($p \leq 0.05$) between the irrigated schemes within each sowing date.

Biomass

The biomass of both Amorgos and Elmo plants was not affected by the sowing date under irrigated scheme, whereas this trait decreased in these varieties significantly when they were sown late (SD3) under non-irrigated scheme. On the other hand, the biomass of Orion was not affected by either the sowing date or the irrigated scheme. The irrigation had significant effect on the biomass of both Elmo and Orion, regardless of sowing date, whereas this effect was significant for Amorgos at the late (SD3) sowing date only. Similarly, Singh et al. (2004) reported that irrigation applied at pre-flowering and pod development stages significantly increased the plant height, pod number per plant, biomass, and seed yield of chickpea. The authors justified these increases by irrigation being applied at these critical stages of crop development. Both Orion and Elmo plants had significantly higher biomass than Amorgos plants, regardless of sowing date and irrigation scheme (except for Elmo and Amorgos at SD2) (Figure 12).

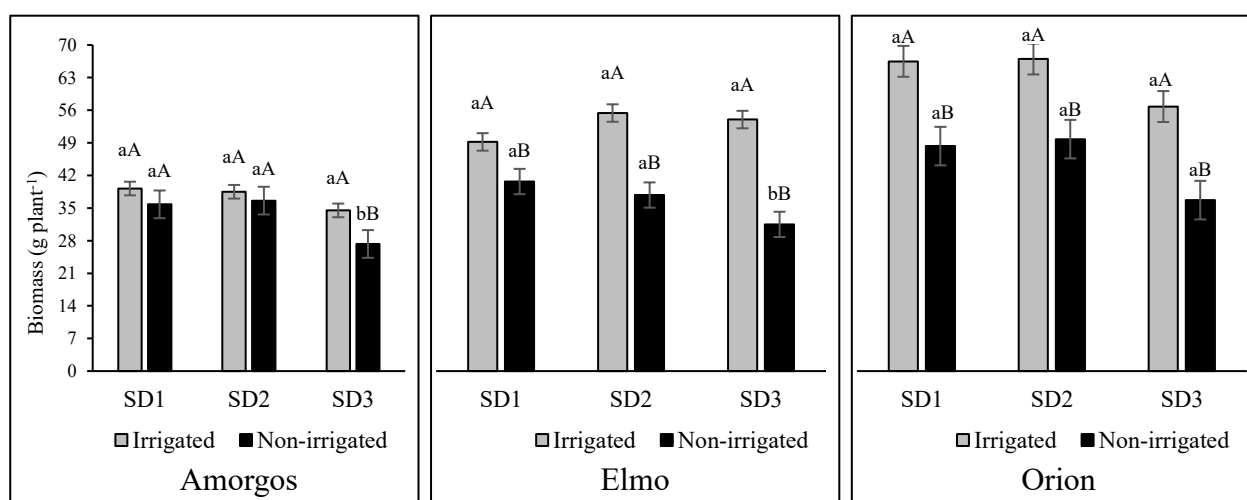


Figure 12. Biomass (g plant⁻¹) of three chickpea varieties (Amorgos, Elmo, and Orion) sown at three different sowing dates (SD1, SD2, and SD3) under supplemental irrigation (irrigated) and rainfed (non-irrigated) conditions. n = 8, $\pm$ SD. Different small letters indicate significant differences ($p \leq 0.05$) among sowing dates within each irrigation scheme. Different capital letters indicate significant differences ($p \leq 0.05$) between the irrigated schemes within each sowing date.

Protein Concentration

The effect of sowing date on the protein concentration in the seeds differed among varieties. The late (SD3) sowing date resulted in significant increase in the protein concentration in the seeds of Elmo under both irrigation schemes and in Amorgos seeds under irrigated scheme. Orion seeds, on the other hand, did not show any measurable differences in this trait among sowing dates or between irrigation schemes. Irrigation increased this trait significantly at SD2 and SD3 in Amorgos and Orion, and at all sowing dates in Elmo. Apart from Amorgos seeds sown early (SD1), there weren't any significant differences in this trait among the studies varieties, regardless of sowing date and irrigation scheme (Figure 13).

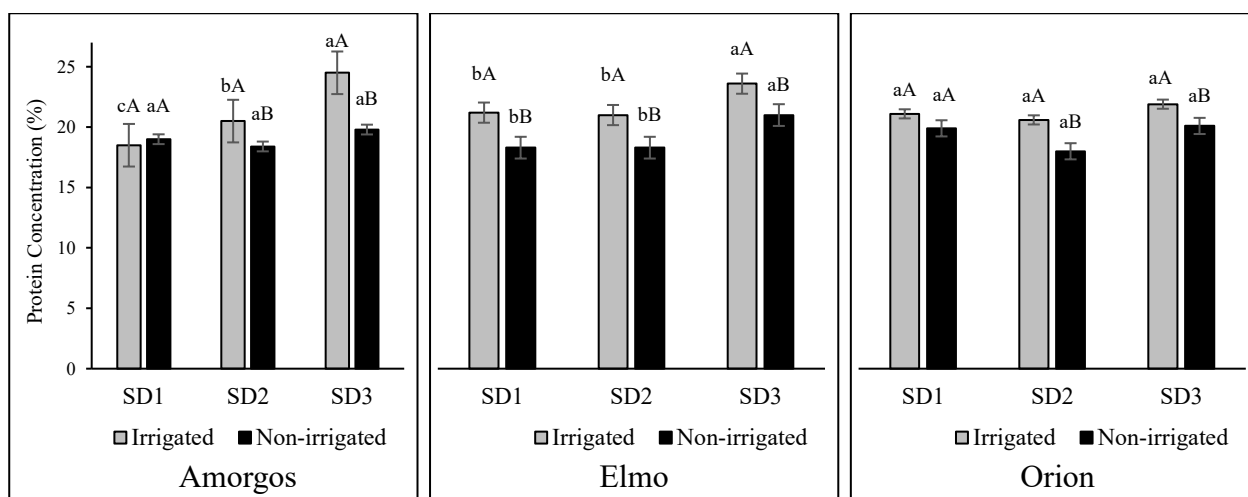


Figure 13. Seed protein concentration (%) of three chickpea varieties (Amorgos, Elmo, and Orion) sown at three different sowing dates (SD1, SD2, and SD3) under supplemental irrigation (irrigated) and rainfed (non-irrigated) conditions. $n = 8$, $\pm$ SD. Different small letters indicate significant differences ($p \leq 0.05$) among sowing dates within each irrigation scheme. Different capital letters indicate significant differences ($p \leq 0.05$) between the irrigated schemes within each sowing date.

Fat Concentration

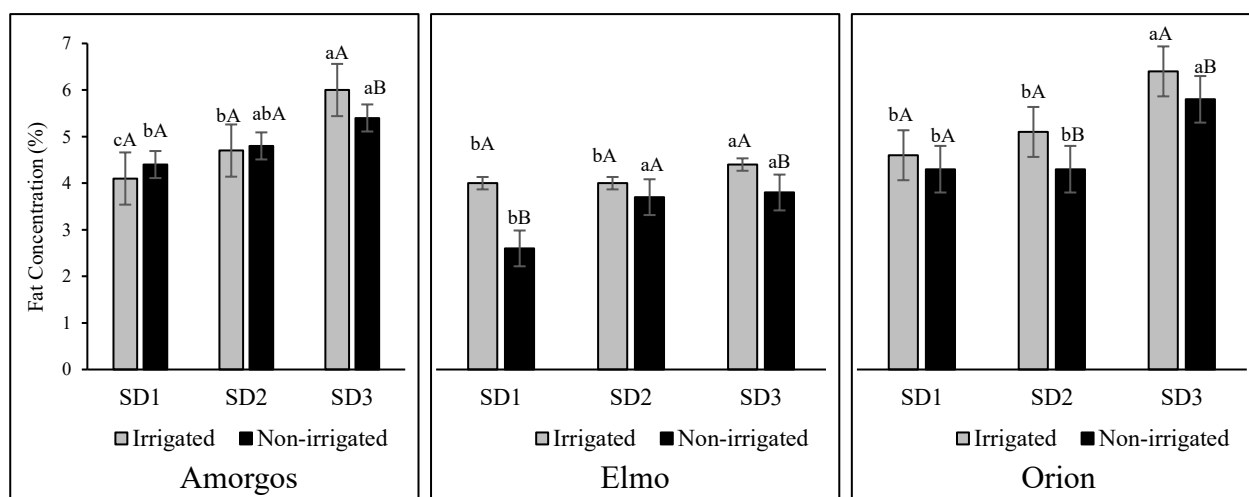


Figure 14. Seed fat concentration (%) of three chickpea varieties (Amorgos, Elmo, and Orion) sown at three different sowing dates (SD1, SD2, and SD3) under supplemental irrigation (irrigated) and rainfed (non-irrigated) conditions. $n = 8$, $\pm$ SD. Different small letters indicate significant differences ($p \leq 0.05$) among sowing dates within each irrigation scheme. Different capital letters indicate significant differences ($p \leq 0.05$) between the irrigated schemes within each sowing date.

The fat concentration in the seeds of all studied varieties sown late (SD3) was significantly higher than their counterparts sown early (SD1), regardless of irrigation scheme. In addition, SD3 resulted in higher fat concentration in the seeds of all varieties as compared to SD2 under irrigated scheme and in Orion seeds under non-irrigated scheme. Irrigation increased this trait at SD1 in Elmo, at SD2 in Orion, and at SD3 in all varieties. The fat concentration in the seeds of Orion was significantly higher than that of Elmo at all sowing dates and under both irrigation schemes. In addition, Amorgos seeds had significantly higher fat concentration than

Elmo seeds at all sowing dates under non-irrigated scheme and at SD3 under irrigated scheme (Figure 14).

Dietary Fiber Concentration

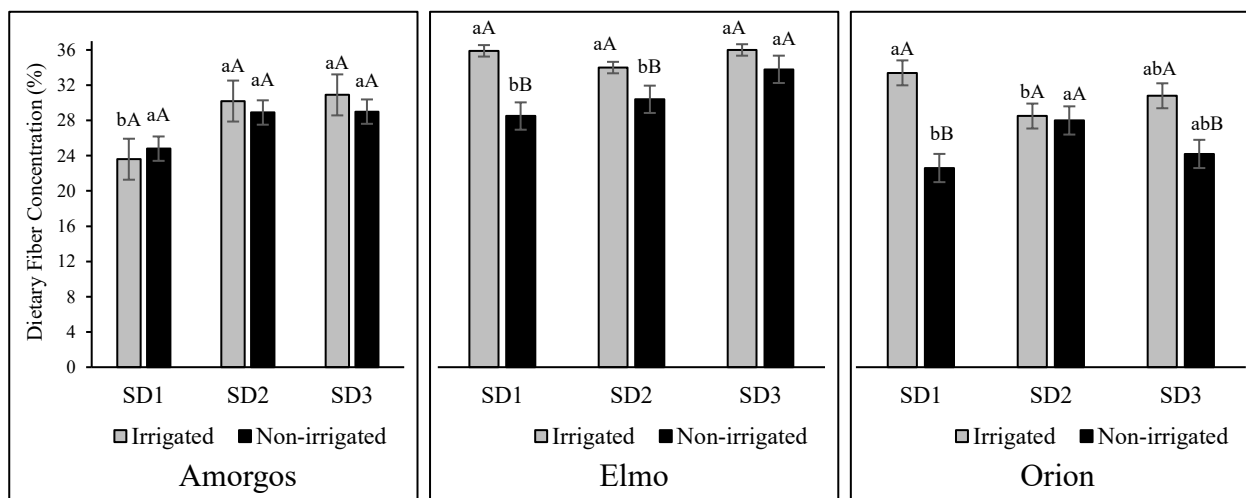


Figure 15. Seed dietary fiber concentration (%) of three chickpea varieties (Amorgos, Elmo, and Orion) sown at three different sowing dates (SD1, SD2, and SD3) under supplemental irrigation (irrigated) and rainfed (non-irrigated) conditions. $n = 8$, $\pm$ SD. Different small letters indicate significant differences ($p \leq 0.05$) among sowing dates within each irrigation scheme. Different capital letters indicate significant differences ($p \leq 0.05$) between the irrigated schemes within each sowing date.

The concentration of dietary fibers in the seeds of the studied varieties showed different responses to the sowing date and to the irrigation scheme. Under both irrigation schemes, the late (SD3) sowing date resulted in the highest concentration of dietary fibers in the seeds of both Amorgos and Elmo. In Orion seeds, SD3 had values of this trait that were statistically similar to the highest values recorded (at SD1 under irrigated scheme, and SD2 under non-irrigated scheme). The irrigation effect was not significant in Amorgos at any sowing date, whereas it increased this trait significantly at SD1 and SD2 in Elmo, and at SD1 and SD3 in Orion. The concentration of dietary fibers in the seeds of Elmo was significantly higher than that of the other varieties, regardless of sowing date and irrigation scheme. Compared to Amorgos, Orion had significantly higher dietary fiber concentration in its seeds at SD1 under irrigated scheme but was significantly lower at all sowing dates under non-irrigated scheme (Figure 15).

4.1.2. The Effects of Nitrogen Application and Rates on The Physiology and Yield of Quinoa under Supplemental Irrigation Conditions

Leaf Area Index

The LAI of Titicaca plants increased significantly under N2 fertilization scheme when irrigation was applied, whereas fertilization with any N dose significantly reduced the LAI under drought stress conditions. In Vikinga, however, and regardless of irrigation scheme, the application of N at any dose did not enhance this trait; it even decreased the LAI under N2 fertilization scheme. Previous research concluded that N application increased the LAI of

quinoa plants that were not subjected to drought stress conditions (Deng, et al., 2024b), which may be primarily due to the role of nitrogen supplementation in enhancing the vegetative growth and the metabolism processes in the plant (Basra et al., 2014). The effect of irrigation was also different between the two varieties. Irrigation significantly increased the LAI of Titicaca plants under N2 fertilization scheme only, whereas irrigated Vikinga plants had significantly higher LAI, regardless of N fertilization scheme (Figure 16). Previously, Bois et al. (2006) reported that the LAI of quinoa plants that were subjected to drought stress decreased by 18%.

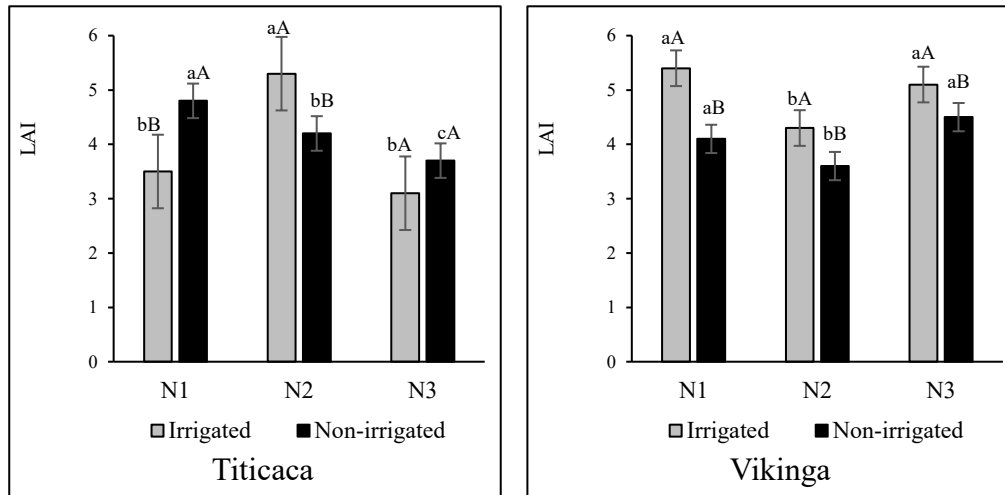


Figure 16. Leaf area index (LAI) of two quinoa varieties (Titicaca and Vikinga) supplied with three different nitrogen fertilization rates (N1, N2, and N3) under supplemental irrigation (irrigated) and rainfed (non-irrigated) conditions. $n = 8$, $\pm$ SD. Different small letters indicate significant differences ($p \leq 0.05$) among fertilization rates within each irrigation scheme. Different capital letters indicate significant differences ($p \leq 0.05$) between the irrigated schemes within each fertilization rate.

Normalized Difference Vegetation Index

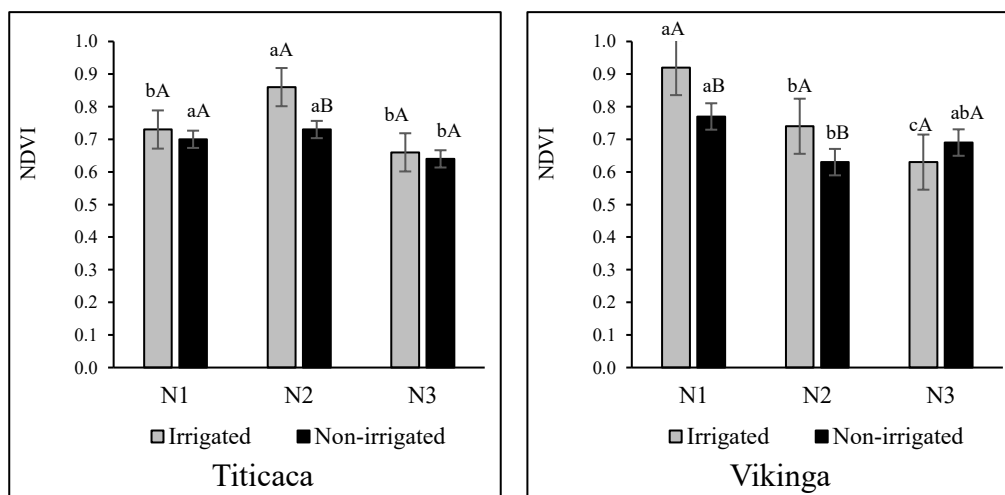


Figure 17. Normalized difference vegetation index (NDVI) of two quinoa varieties (Titicaca and Vikinga) supplied with three different nitrogen fertilization rates (N1, N2, and N3) under supplemental irrigation (irrigated) and rainfed (non-irrigated) conditions. $n = 8$, $\pm$ SD. Different small letters indicate significant differences ($p \leq 0.05$) among fertilization rates within each irrigation scheme. Different capital letters indicate significant differences ($p \leq 0.05$) between the irrigated schemes within each fertilization rate.

Under irrigated scheme, N2 fertilization scheme significantly increased the normalized difference vegetation index (NDVI) of Titicaca plants, whereas this trait did not respond to any N dose under drought stress conditions. Furthermore, Vikinga plants did not show any enhancements in this trait by the application of N, regardless of irrigation scheme. Irrigation significantly increased the NDVI of Titicaca plants under N2 fertilization scheme only, whereas it did so under both N1 and N2 schemes for Vikinga plants (Figure 17).

Total Chlorophyll Content

The total chlorophyll content in irrigated Titicaca plants increased significantly when N fertilizer was applied (N2 and N3 schemes) as compared to the control treatment, whereas this trait did not respond to N fertilization under drought stress conditions. In Vikinga, the application of N fertilizer at any dose did not result in any enhancements in the total chlorophyll content, regardless of irrigation scheme. Irrigation significantly increased the total chlorophyll content in Titicaca under both N2 and N3 fertilization schemes, whereas only under N3 fertilization scheme in Vikinga (Figure 18). Forouzandeh et al. (2024) also reported a significant reduction in the total chlorophyll content of quinoa plants under drought stress conditions.

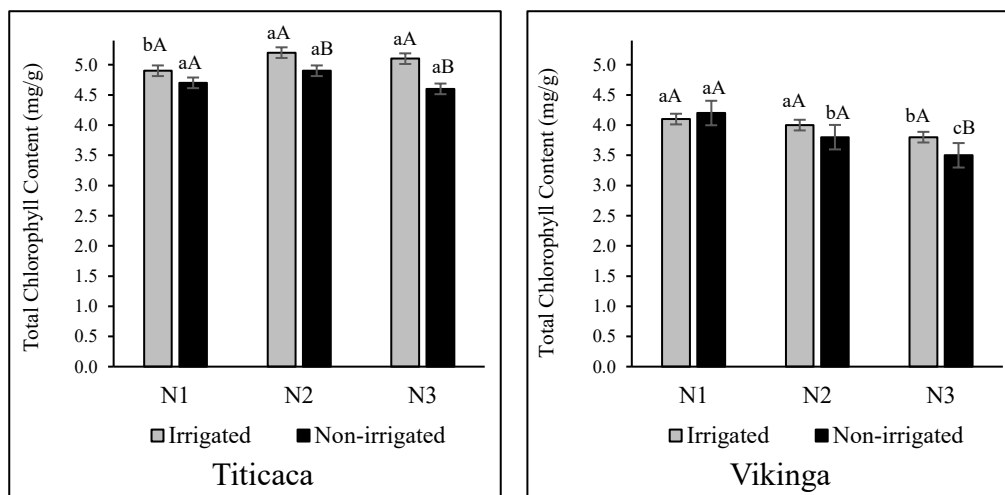


Figure 18. Total chlorophyll content (mg/g) of two quinoa varieties (Titicaca and Vikinga) supplied with three different nitrogen fertilization rates (N1, N2, and N3) under supplemental irrigation (irrigated) and rainfed (non-irrigated) conditions. $n = 8$, $\pm$ SD. Different small letters indicate significant differences ($p \leq 0.05$) among fertilization rates within each irrigation scheme. Different capital letters indicate significant differences ($p \leq 0.05$) between the irrigated schemes within each fertilization rate.

Total Carotenoid Content (mg/g)

Under irrigated scheme, the application of 75 kg N/ha (N2) significantly increased the total carotenoid content in both varieties as compared to the control (N1) treatment, whereas the application of 150 kg N/ha (N3) increased this trait in Titicaca only. Under drought stress conditions, the application of either dose of N did not enhance the total carotenoid content in any of the two varieties. The total carotenoid content was significantly higher in drought-stressed plants of both varieties under N1 fertilization scheme; however, the difference was insignificant under N2 fertilization scheme (Figure 19).

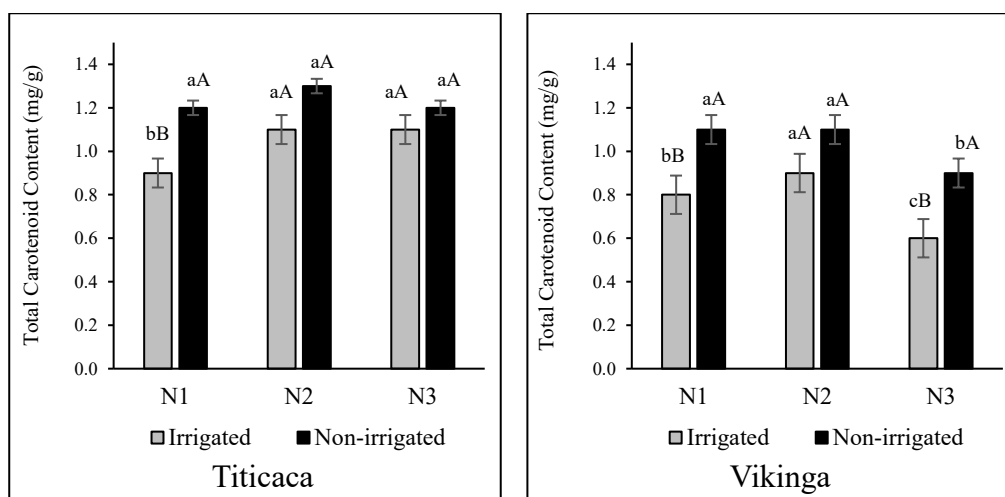


Figure 19. Total carotenoid content (mg/g) of two quinoa varieties (Titicaca and Vikinga) supplied with three different nitrogen fertilization rates (N1, N2, and N3) under supplemental irrigation (irrigated) and rainfed (non-irrigated) conditions. $n = 8$, $\pm$ SD. Different small letters indicate significant differences ($p \leq 0.05$) among fertilization rates within each irrigation scheme. Different capital letters indicate significant differences ($p \leq 0.05$) between the irrigated schemes within each fertilization rate.

Plant Height cm

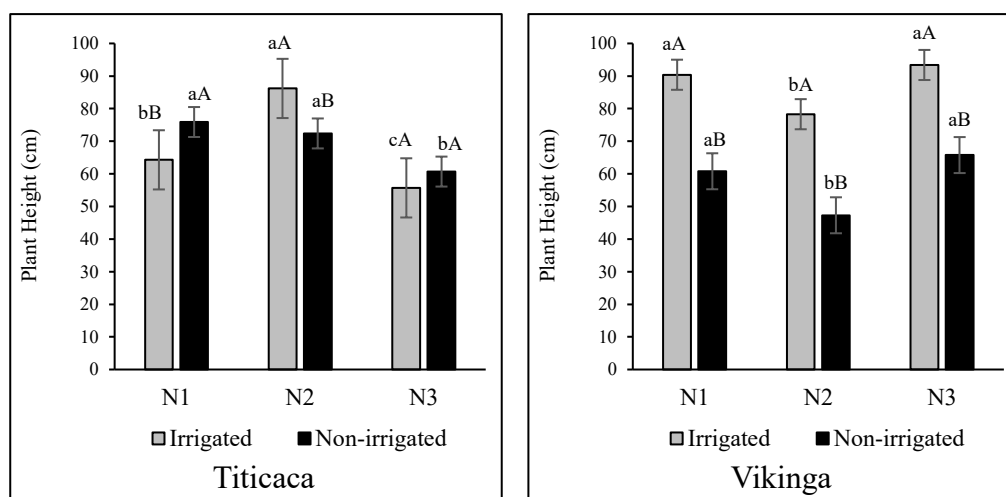


Figure 20. Plant height (cm) of two quinoa varieties (Titicaca and Vikinga) supplied with three different nitrogen fertilization rates (N1, N2, and N3) under supplemental irrigation (irrigated) and rainfed (non-irrigated) conditions. $n = 8$, $\pm$ SD. Different small letters indicate significant differences ($p \leq 0.05$) among fertilization rates within each irrigation scheme. Different capital letters indicate significant differences ($p \leq 0.05$) between the irrigated schemes within each fertilization rate.

The two varieties responded differently to N application when irrigation was provided. In Titicaca, N2 resulted in significant increase in the plant height, whereas N3 caused significant reduction in this trait. In Vikinga, the application of N at any rate did not affect the plant height. Under drought conditions, this trait was not enhanced by any dose of N. Sun et al., (2025) also revealed that nitrogen level has a significant influence on the plant height of quinoa plants. The effect of irrigation was also different between the two varieties. Irrigation significantly increased the plant height of Vikinga plants, regardless of N application, whereas it did so in Titicaca under N2 fertilization scheme only (Figure 20). Similarly, Pathan et al.

(2023) reported that different quinoa varieties responded differently to irrigation in terms of plant height, where some varieties had increased, while others had decreased plant height under drought stress conditions.

Biomass kg/ha

Under irrigated scheme, the application of 75 kg N/ha (N2) increased the biomass of both varieties significantly. Furthermore, the application of 150 kg N/ha (N3) increased this trait significantly in Vikinga, but not in Titicaca. Under drought stress conditions, on the other hand, the application of N did not increase the biomass of either variety. Other reports concluded that some quinoa varieties had elevated biomass under higher N rate application (e.g., Jerez et al., 2023), while others responded negatively (Hassan et al., 2022). Irrigation increased the biomass of Vikinga significantly, regardless of N treatment, whereas it did so only for N2 treatment in Titicaca, indicating that the biomass of the two varieties responded differently to the interaction of irrigation and N fertilization schemes (Figure 21).

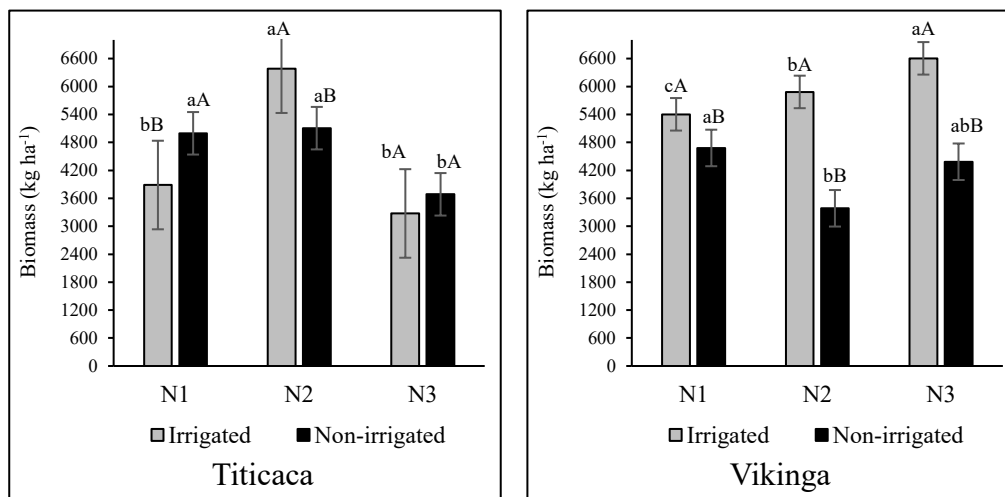


Figure 21. Biomass (kg ha⁻¹) of two quinoa varieties (Titicaca and Vikinga) supplied with three different nitrogen fertilization rates (N1, N2, and N3) under supplemental irrigation (irrigated) and rainfed (non-irrigated) conditions. n = 8, ±SD. Different small letters indicate significant differences (p ≤ 0.05) among fertilization rates within each irrigation scheme. Different capital letters indicate significant differences (p ≤ 0.05) between the irrigated schemes within each fertilization rate.

Seed Yield

The application of 75 kg N/ha (N2) increased the seed yield of both varieties significantly under irrigated scheme, compared to the control (N1) counterpart. The application of higher (N3) dose of N did not increase the yield of either variety compared to N2 treatment. Under drought stress scheme, N2 resulted in higher seed yield in Titicaca only. N3 caused a significant reduction of the seed yield of both varieties compared to the control (N1) treatment. Optimizing nitrogen level for better growth, physiology and yield of quinoa while maintaining environmental safety is critical for sustainable production. Several studies suggest that nitrogen applications rates of 120 to 160 kg ha⁻¹ can be an optimum level for obtaining maximum growth, yield and improved nitrogen uptake and use efficiency (Deng et al., 2024b; Li et al., 2025; Sun et al., 2025) though optimization strategies are location-specific and can be tailored according to particular agroecological situations (Pradhan et al., 2025).

Excessive nitrogen fertilizer applications have limited effects on enhancing quinoa yield and/or even detrimental effects (Wang et al., 2022).

Irrigation increased the seed yield of both varieties under N2 fertilization scheme, but only of Vikinga under N3 fertilization scheme, whereas the seed yield of both varieties was significantly lower under irrigated scheme when no N fertilizer (N1) was applied (Figure 22). Response to drought stress is genotype-dependent; some genotypes did not show measurable yield losses under drought stress conditions, while others di (Maestro-Gaitán et al., 2022).

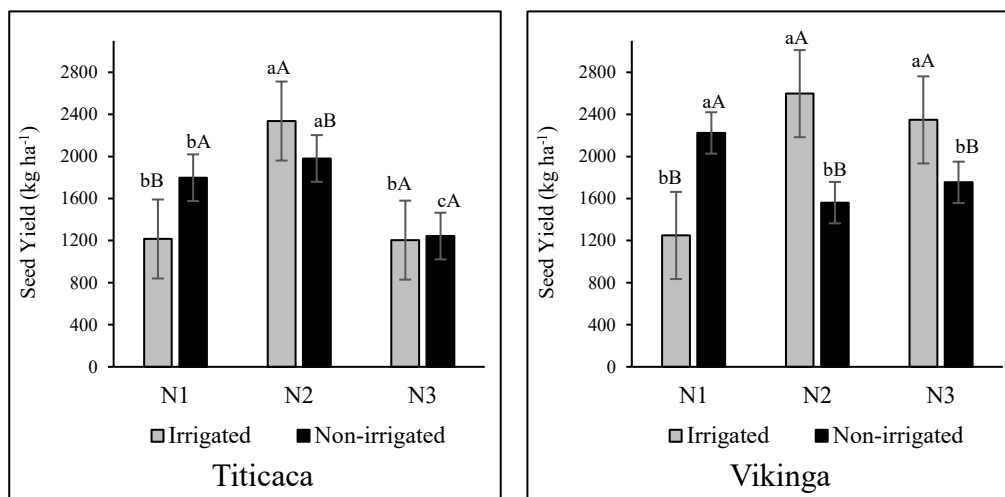


Figure 22. Seed yield (kg ha^{-1}) of two quinoa varieties (Titicaca and Vikinga) supplied with three different nitrogen fertilization rates (N1, N2, and N3) under supplemental irrigation (irrigated) and rainfed (non-irrigated) conditions. $n = 8$, $\pm\text{SD}$. Different small letters indicate significant differences ($p \leq 0.05$) among fertilization rates within each irrigation scheme. Different capital letters indicate significant differences ($p \leq 0.05$) between the irrigated schemes within each fertilization rate.

4.2. Controlled Environment Experiments

4.2.1. The Effects of Exogenous Application of Hydrogen Peroxide on The Morphophysiology and Biochemistry of Soybean under Severe Drought Stress Conditions

Root Length

After 3 days of drought stress application, the root length of both genotypes was significantly higher in all drought-stressed treatments than that of control treatment. In Coraline, the treatment which was sprayed with 10 mM H_2O_2 had significantly shorter roots (by 3.5%) compared to the treatment that was not sprayed. On the other hand, Speeda plants that received 1 mM H_2O_2 foliar spray had significantly longer roots (by 3.6%) compared to the non-sprayed counterpart. Increased root length under drought stress conditions can help the plants acquire more water and nutrients from deeper soil levels (Zegada-Lizarazu and Monti, 2019). Li et al. (2018) concluded that H_2O_2 enhances root growth by increasing ABA levels. It was previously reported that the roots and seedlings of sweet potato responded positively to the application of H_2O_2 at levels between 0.5 and 2.5 mM, but negatively at levels of 5 mM or more (Deng et al., 2012). Within the group of treatments that was allowed to recover from drought, Coraline plants that were sprayed with either 1 mM or 5 mM H_2O_2 and Speeda plants

that were sprayed with 1 mM H₂O₂ had significantly higher root lengths compared to their counterpart treatments that did not receive foliar spray. Within the group of treatments that were continuously under drought stress conditions, the root length of Coraline plants that were sprayed with either 1 mM or 5 mM H₂O₂ was significantly higher than the non-sprayed counterpart, whereas the foliar spray did not enhance this trait for Speeda plants at this point. At the end of the podding stage, the root length of all the treatments that received any concentration of H₂O₂ foliar spray was higher than the control treatments of both genotypes (Figure 23).

After 3 days of drought stress application, the root length was not measurably different between the studied genotypes, regardless of H₂O₂ treatment and concentration. Later however, Coraline had longer roots in most treatments, especially within the group of treatments that were allowed to recover from drought. This last observation was more obvious at the end of the podding stage, where the root length of all treatments of Coraline was significantly higher than the counterpart treatments of Speeda (Figure 23).

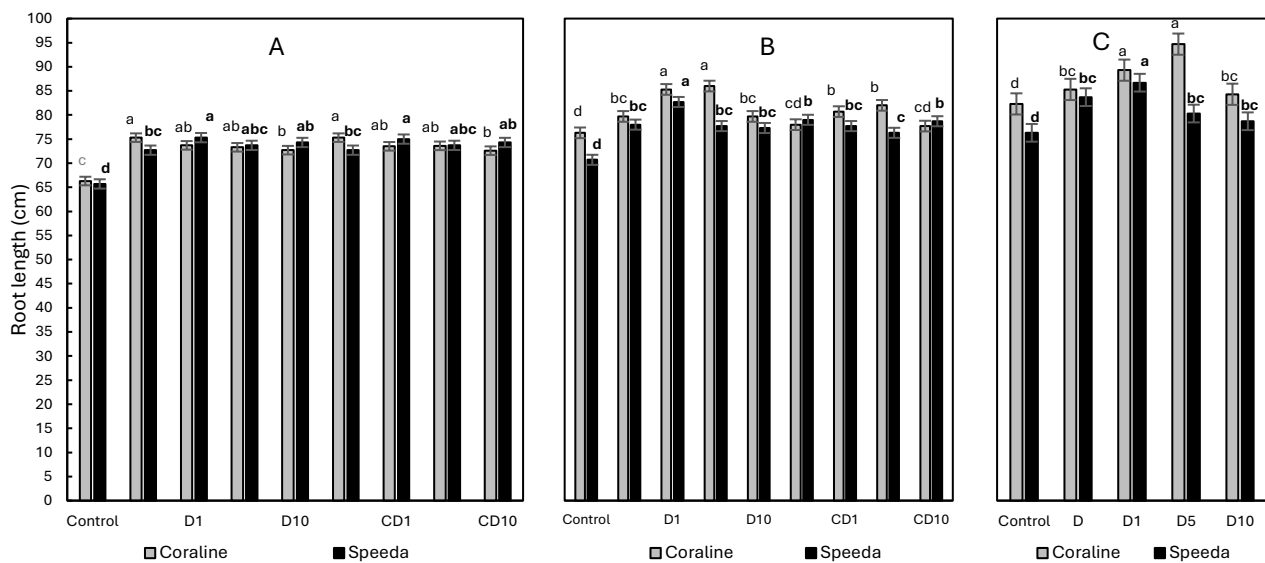


Figure 23. Root length (cm) of two soybean genotypes (Coraline and Speeda) at 3 different sampling dates (A: 3 days after drought stress application at R1 stage, B: 3 days after R3 stage started, C: at the end of R4 stage) as affected by hydrogen peroxide foliar spray application under drought stress conditions (D: drought from R1 till R2 stage, D1: drought from R1 till R2 stage + 1mM hydrogen peroxide, D5: drought from R1 till R2 stage + 5mM hydrogen peroxide, D10: drought from R1 till R2 stage + 10mM hydrogen peroxide, CD: continuous drought starting from R1 stage, CD1: continuous drought starting from R1 stage + 1mM hydrogen peroxide, CD5: continuous drought starting from R1 stage + 5mM hydrogen peroxide, CD10: continuous drought starting from R1 stage + 10mM hydrogen peroxide). All values are the means of 3 replicates (columns) $\pm$ standard errors (vertical whiskers). In each genotype, different letters indicate significant differences at .05 level as indicated by Duncan's multiple range test.

Shoot Length

The shoot length of both genotypes significantly decreased as a result of drought stress application. However, the H₂O₂ foliar spray application, of any concentration in Coraline and of 1 mM in Speeda, could significantly enhance this trait. Similar conclusion was also reported by Bashir et al. (2019). When plants of both genotypes were relieved from drought

and allowed to recover, the groups of treatments that received any concentration of H₂O₂ foliar spray showed significantly higher shoot length compared to the non-sprayed counterparts. Under continuous drought conditions, only the concentrations of 5 mM and 1 mM H₂O₂ foliar spray could result in better shoot lengths in Coraline and Speeda, respectively. At the end of podding stage, all Coraline plants that received H₂O₂ foliar spray showed significantly better shoot length (better even than the control), whereas that positive effect was noticed only on the treatment of Speeda that received 1 mM H₂O₂ foliar spray, where the shoot length was 9.1% higher than that of the treatment that was not sprayed (D) and 4.8% higher than that of the control treatment (Figure 24).

Regardless of drought and H₂O₂ application, the shoot length of Speeda was significantly higher than that of Coraline throughout the whole experimental period.

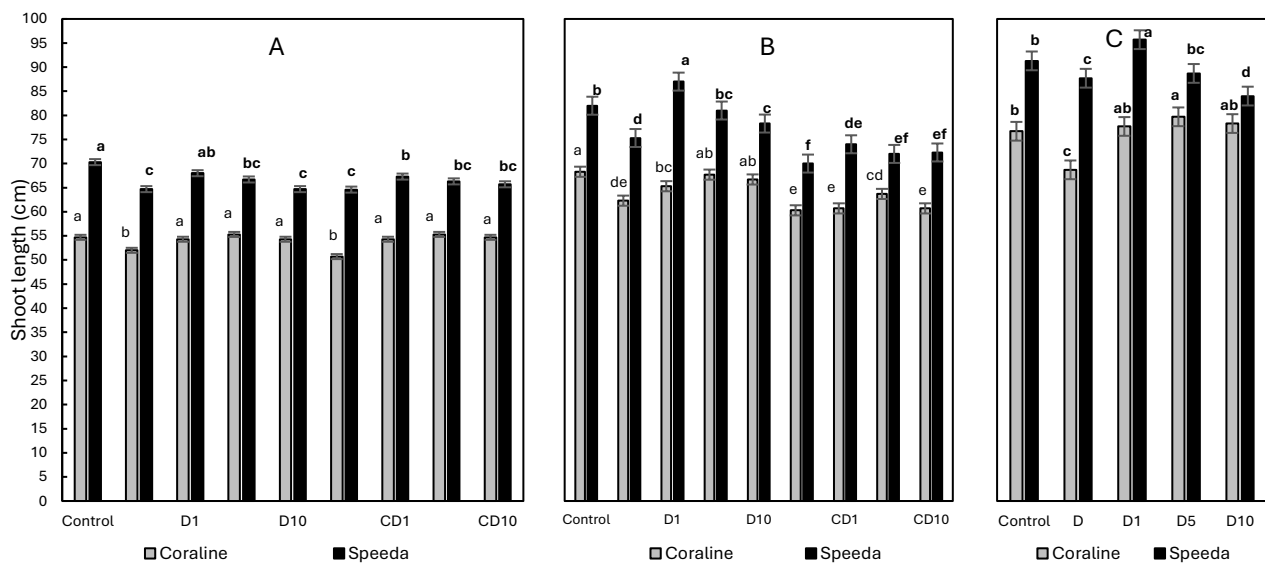


Figure 24. Shoot length (cm) of two soybean genotypes (Coraline and Speeda) at 3 different sampling dates (A: 3 days after drought stress application at R1 stage, B: 3 days after R3 stage started, C: at the end of R4 stage) as affected by hydrogen peroxide foliar spray application under drought stress conditions (D: drought from R1 till R2 stage, D1: drought from R1 till R2 stage + 1mM hydrogen peroxide, D5: drought from R1 till R2 stage + 5mM hydrogen peroxide, D10: drought from R1 till R2 stage + 10mM hydrogen peroxide, CD: continuous drought starting from R1 stage, CD1: continuous drought starting from R1 stage + 1mM hydrogen peroxide, CD5: continuous drought starting from R1 stage + 5mM hydrogen peroxide, CD10: continuous drought starting from R1 stage + 10mM hydrogen peroxide). All values are the means of 3 replicates (columns) $\pm$ standard errors (vertical whiskers). In each genotype, different letters indicate significant differences at .05 level as indicated by Duncan's multiple range test.

Specific leaf area

Drought stress application resulted in significant reductions in the specific leaf area (SLA) of both genotypes as compared to control counterparts. However, the application of H₂O₂ foliar spray significantly increased SLA, regardless of its concentration. Compared to control plants, the application of 5 mM and 10 mM H₂O₂ foliar spray on Coraline resulted in significantly higher SLA (by 26.7% and 12.3%, respectively) after 3 days of drought application, whereas only the 1 mM H₂O₂ concentration could enhance this trait in Speeda. Under continuous drought stress conditions, the application of H₂O₂ foliar spray could

significantly increase SLA in both genotypes as compared to the non-sprayed counterparts. Recovering Coraline plants sprayed with either 5 mM or 10 mM H₂O₂ could maintain higher SLA values as compared to control plants, whereas Speeda plants could not. Similar findings were observed at the end of the podding stage (Figure 25). The capacity of light intercepted by plants, and thus of photosynthetic rate is measurably affected by the plant's leaf area (Verma et al., 2020). It is well documented that drought stress results in reduced leaf area (e.g., Gavili et al. (2019). Exogenous spray of H₂O₂ could enhance the leaf area of soybean plants (Basal and Szabó, 2020).

At all sampling dates, SLA of Speeda was higher in control and drought-stressed treatments that did not receive any foliar spray; however, Coraline plants that were sprayed with either 5 mM or 10 mM H₂O₂ had higher SLA.

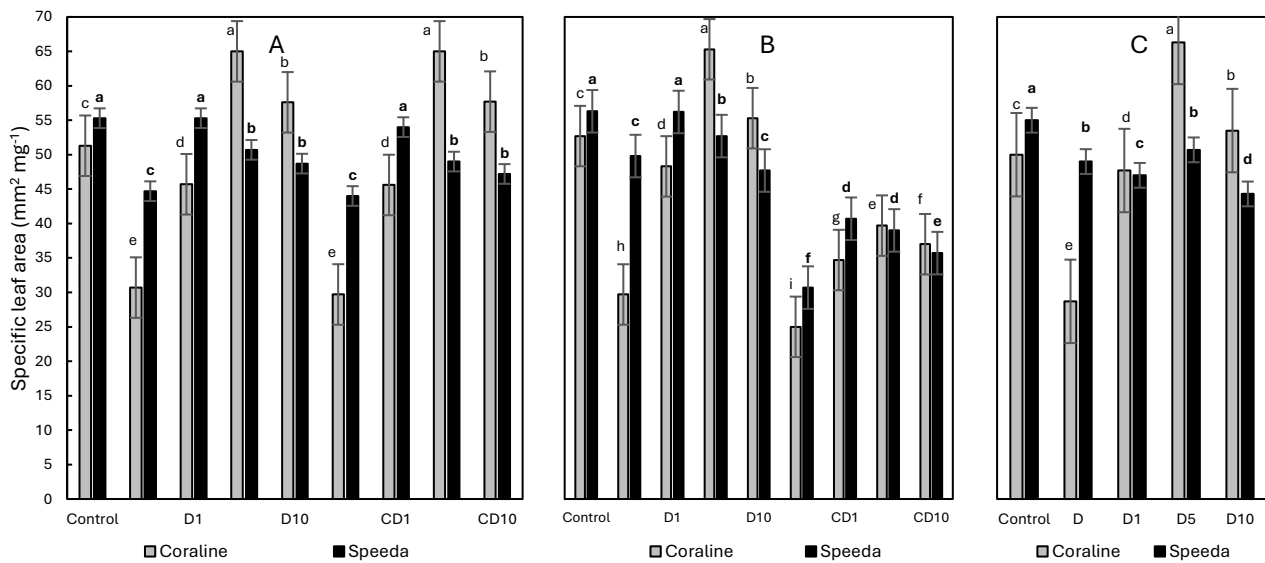


Figure 25. Specific leaf area (mm² mg⁻¹) of two soybean genotypes (Coraline and Speeda) at 3 different sampling dates (A: 3 days after drought stress application at R1 stage, B: 3 days after R3 stage started, C: at the end of R4 stage) as affected by hydrogen peroxide foliar spray application under drought stress conditions (D: drought from R1 till R2 stage, D1: drought from R1 till R2 stage + 1mM hydrogen peroxide, D5: drought from R1 till R2 stage + 5mM hydrogen peroxide, D10: drought from R1 till R2 stage + 10mM hydrogen peroxide, CD: continuous drought starting from R1 stage, CD1: continuous drought starting from R1 stage + 1mM hydrogen peroxide, CD5: continuous drought starting from R1 stage + 5mM hydrogen peroxide, CD10: continuous drought starting from R1 stage + 10mM hydrogen peroxide). All values are the means of 3 replicates (columns) ± standard errors (vertical whiskers). In each genotype, different letters indicate significant differences at .05 level as indicated by Duncan's multiple range test.

Optimal photochemical efficiency of PSII

Drought stress caused a significant reduction in this trait after 3 days of application on both genotypes (by 26% and 21.1% in Coraline and Speeda, respectively). However, applying the foliar spray of all concentrations on Coraline and of 1mM and 5 mM on Speeda led to significant enhancement in Fv/Fm. Compared to the treatments that were subjected to continuous drought, the group of treatments where the drought was relieved was able to maintain higher Fv/Fm values, with and without the application of H₂O₂ foliar spray and regardless of its concentration. Fv/Fm was significantly higher (by 8.8%) when 5mM H₂O₂

foliar spray was applied to the recovering Coraline plants after 3 days of recovery compared to the non-sprayed recovering plants, whereas the foliar spray had no significant enhancement in Speeda recovering plants. Similar results were recorded at the end of the podding stage, where Fv/Fm values were not affected by the foliar spray on Speeda plants but were significantly better when 1mM or 5mM H₂O₂ was applied on Coraline plants (Figure 26). It was previously reported that a key factor of plant's response to variations in the surrounding environment is the chlorophyll fluorescence (Dai et al., 2009). Under drought stress conditions, leaves absorb and translocate less energy to PSII, leading to inhibited plant development (Rahbarian et al., 2011). Muhammad et al. (2021) reported that Fv/Fm significantly decreased under PEG-induced drought stress.

After drought application, Speeda plants had significantly higher Fv/Fm values in all treatments, except for the treatments where 10 mM H₂O₂ was applied (where the Fv/Fm values of Speeda was still higher, yet not significantly). However, there were no measurable differences between the two genotypes after the recovery process, i.e. Coraline plants were able to retain comparable Fv/Fm values when the plants had the chance to recover with and without foliar spray application (Figure 26).

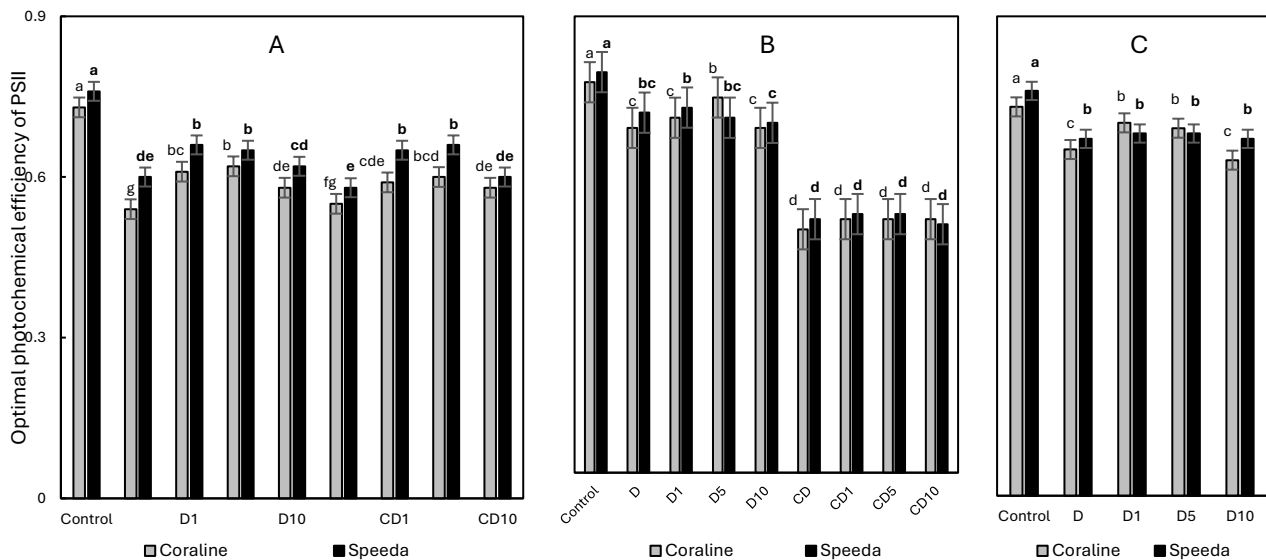


Figure 26. Optimal photochemical efficiency of PSII of two soybean genotypes (Coraline and Speeda) at 3 different sampling dates (A: 3 days after drought stress application at R1 stage, B: 3 days after R3 stage started, C: at the end of R4 stage) as affected by hydrogen peroxide foliar spray application under drought stress conditions (D: drought from R1 till R2 stage, D1: drought from R1 till R2 stage + 1mM hydrogen peroxide, D5: drought from R1 till R2 stage + 5mM hydrogen peroxide, D10: drought from R1 till R2 stage + 10mM hydrogen peroxide, CD: continuous drought starting from R1 stage, CD1: continuous drought starting from R1 stage + 1mM hydrogen peroxide, CD5: continuous drought starting from R1 stage + 5mM hydrogen peroxide, CD10: continuous drought starting from R1 stage + 10mM hydrogen peroxide). All values are the means of 3 replicates (columns) $\pm$ standard errors (vertical whiskers). In each genotype, different letters indicate significant differences at .05 level as indicated by Duncan's multiple range test.

Actual photochemical efficiency of PSII

The application of drought stress significantly reduced the actual photochemical efficiency of PSII of both genotypes 3 days after its application, regardless of H₂O₂ application and concentration. However, the exogenous application of H₂O₂ at any concentration significantly enhanced this trait in both genotypes as compared to the non-sprayed, drought-stressed treatment. After terminating the drought, the treatments that were sprayed with any concentration of H₂O₂ were still significantly higher in terms of yield as compared to the non-sprayed treatment. The group of treatments that were kept under drought stress conditions had significantly lower values of this trait. Within this group, the plants that received either 1 or 5, but not 10 mM H₂O₂, had significantly higher values than the treatment that did not receive any foliar H₂O₂. At the end of the podding stage, the actual photochemical efficiency of PSII of the treatments that received any concentration of H₂O₂ was still significantly higher than that of the treatment that did not receive H₂O₂ spray (Figure 27).

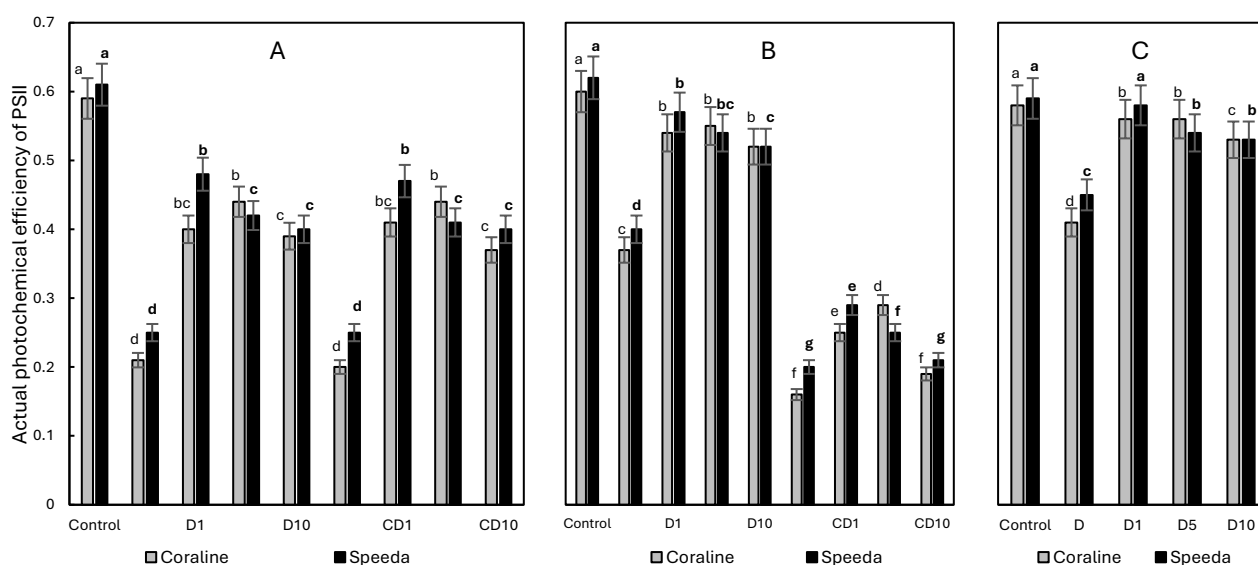


Figure 27. Actual photochemical efficiency of PSII of two soybean genotypes (Coraline and Speeda) at 3 different sampling dates (A: 3 days after drought stress application at R1 stage, B: 3 days after R3 stage started, C: at the end of R4 stage) as affected by hydrogen peroxide foliar spray application under drought stress conditions (D: drought from R1 till R2 stage, D1: drought from R1 till R2 stage + 1mM hydrogen peroxide, D5: drought from R1 till R2 stage + 5mM hydrogen peroxide, D10: drought from R1 till R2 stage + 10mM hydrogen peroxide, CD: continuous drought starting from R1 stage, CD1: continuous drought starting from R1 stage + 1mM hydrogen peroxide, CD5: continuous drought starting from R1 stage + 5mM hydrogen peroxide, CD10: continuous drought starting from R1 stage + 10mM hydrogen peroxide). All values are the means of 3 replicates (columns) $\pm$ standard errors (vertical whiskers). In each genotype, different letters indicate significant differences at .05 level as indicated by Duncan's multiple range test.

Chlorophyll-a

After 3 days of drought stress application, the chlorophyll-a content significantly decreased in both genotypes, regardless of H₂O₂ application and concentration. In the drought-susceptible genotype Coraline, the treatments which were allowed to recover from drought stress had significantly higher chla content compared to the treatments which suffered from continuous drought stress. Among these treatments, the foliar application of H₂O₂, regardless

of its concentration, led to significantly higher chl *a* compared to the treatment where the plants were allowed to recover without H₂O₂ foliar spray. The foliar spray, however, did not have measurable effects on the chl *a* content of the treatments which suffered from continuous drought. The foliar spray had no significant effect on the chl *a* content in the drought-tolerant genotype Speeda; however, the group of treatments which was allowed to recover from drought stress had significantly higher chl *a* content compared to the group which suffered from continuous drought. At the end of the podding stage, the control treatment had significantly higher chl *a* content than the drought-stressed treatments (by 54% and 36% in Coraline and Speeda, respectively), and the foliar spray had no measurable effect (Figure 28). H₂O₂ foliar spray can protect the chloroplast under drought stress conditions, resulting in enhanced chlorophyll content (Abbas and Mohamed, 2011; Liu et al., 2010b).

Under drought stress conditions, the chl *a* content in Speeda was significantly higher than in Coraline at all 3 sampling dates, regardless of H₂O₂ application and concentration.

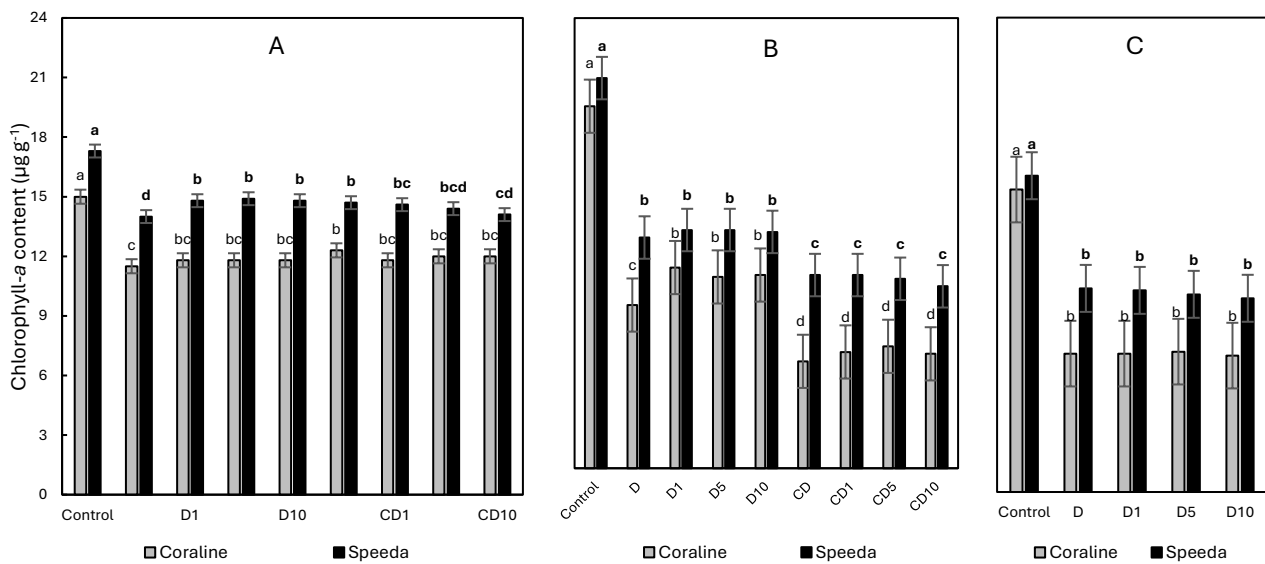


Figure 28. Chlorophyll-*a* content ($\mu\text{g g}^{-1}$) of two soybean genotypes (Coraline and Speeda) at 3 different sampling dates (A: 3 days after drought stress application at R1 stage, B: 3 days after R3 stage started, C: at the end of R4 stage) as affected by hydrogen peroxide foliar spray application under drought stress conditions (D: drought from R1 till R2 stage, D1: drought from R1 till R2 stage + 1mM hydrogen peroxide, D5: drought from R1 till R2 stage + 5mM hydrogen peroxide, D10: drought from R1 till R2 stage + 10mM hydrogen peroxide, CD: continuous drought starting from R1 stage, CD1: continuous drought starting from R1 stage + 1mM hydrogen peroxide, CD5: continuous drought starting from R1 stage + 5mM hydrogen peroxide, CD10: continuous drought starting from R1 stage + 10mM hydrogen peroxide). All values are the means of 3 replicates (columns) $\pm$ standard errors (vertical whiskers). In each genotype, different letters indicate significant differences at .05 level as indicated by Duncan's multiple range test.

Chlorophyll-b

The application of drought stress resulted in significant reduction in the chl *b* content in both genotypes. The foliar H₂O₂ spray could not alleviate that effect. However, the recovered plants of both genotypes had significantly higher content of chl *b* as compared to the plants where drought was continuous. Moreover, the application of H₂O₂ spray on the recovering plants of both genotypes increased the chl *b* content; that increase was significant when 1mM or 5mM of H₂O₂ foliar spray was applied. The foliar spray, on the other hand, did not result in significant enhancements in this trait under continuous drought stress conditions. At the end of the podding stage, the chl *b* content was significantly higher in Coraline (by 14.7%) and Speeda plants (by 7.9%) which were sprayed with 5mM and 1mM of H₂O₂, respectively compared to the non-sprayed counterparts (Figure 29).

Speeda plants had significantly higher chl *b* content under drought stress conditions at all sampling dates.

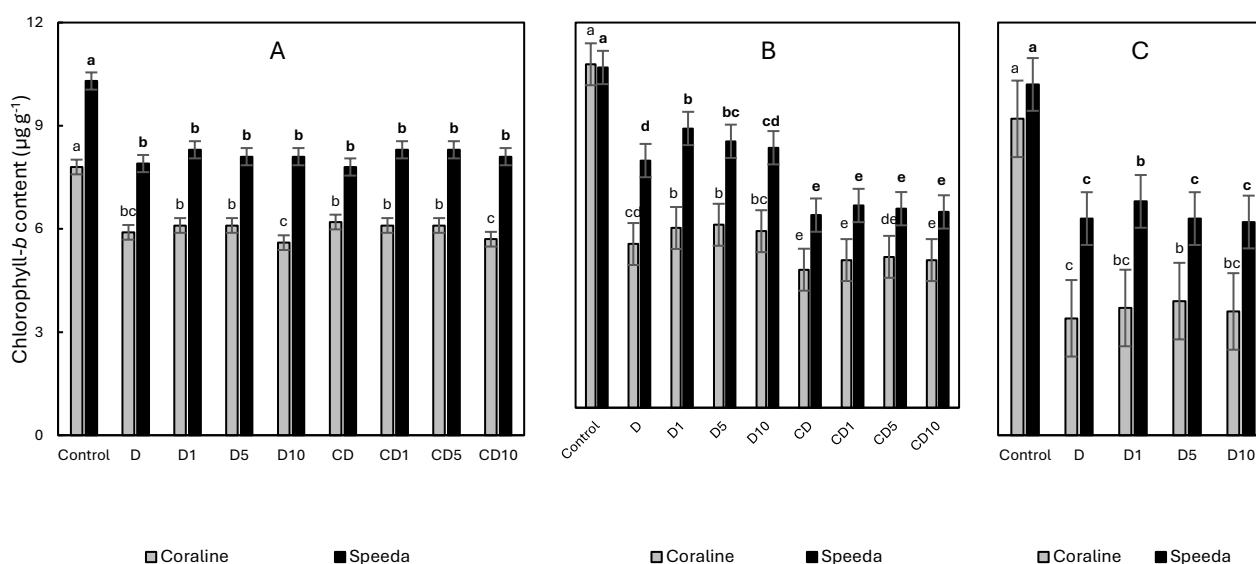


Figure 29. Chlorophyll-*b* content ($\mu\text{g g}^{-1}$) of two soybean genotypes (Coraline and Speeda) at 3 different sampling dates (A: 3 days after drought stress application at R1 stage, B: 3 days after R3 stage started, C: at the end of R4 stage) as affected by hydrogen peroxide foliar spray application under drought stress conditions (D: drought from R1 till R2 stage, D1: drought from R1 till R2 stage + 1mM hydrogen peroxide, D5: drought from R1 till R2 stage + 5mM hydrogen peroxide, D10: drought from R1 till R2 stage + 10mM hydrogen peroxide, CD: continuous drought starting from R1 stage, CD1: continuous drought starting from R1 stage + 1mM hydrogen peroxide, CD5: continuous drought starting from R1 stage + 5mM hydrogen peroxide, CD10: continuous drought starting from R1 stage + 10mM hydrogen peroxide). All values are the means of 3 replicates (columns) $\pm$ standard errors (vertical whiskers). In each genotype, different letters indicate significant differences at .05 level as indicated by Duncan's multiple range test.

Total carotenoids

Significant decrease in the total carotenoid (chlxc) content was recorded in both genotypes (by 28% and 35.5% in Coraline and Speeda, respectively) as a consequence of drought stress application. Except for the application of 10 mM H₂O₂ on Coraline plants, the chlxc content was significantly increased by the H₂O₂ foliar spray on both genotypes. The recovered plants of both genotypes had significantly higher chlxc content compared to the continuously drought-stressed counterparts. In Coraline plants, 1mM H₂O₂ foliar spray on the recovering plants of Coraline significantly increased chlxc compared to the non-sprayed recovering plants, whereas the chlxc of recovering Speeda plants was significantly increased by the application of any concentration of H₂O₂. On the other hand, the foliar spray had no measurable effects on the chlxc of the plants that were not allowed to recover from both genotypes. Interestingly, the chlxc at the end of the podding stage was significantly higher in Speeda plants that were sprayed with 1mM H₂O₂ as compared to the recovering plants that were not sprayed, whereas this trait did not have measurable differences in Coraline at the same period (Figure 30).

Regardless of the drought application and the H₂O₂ application and concentration, the chlxc content was significantly higher in Speeda than in Coraline plants at all sampling dates.

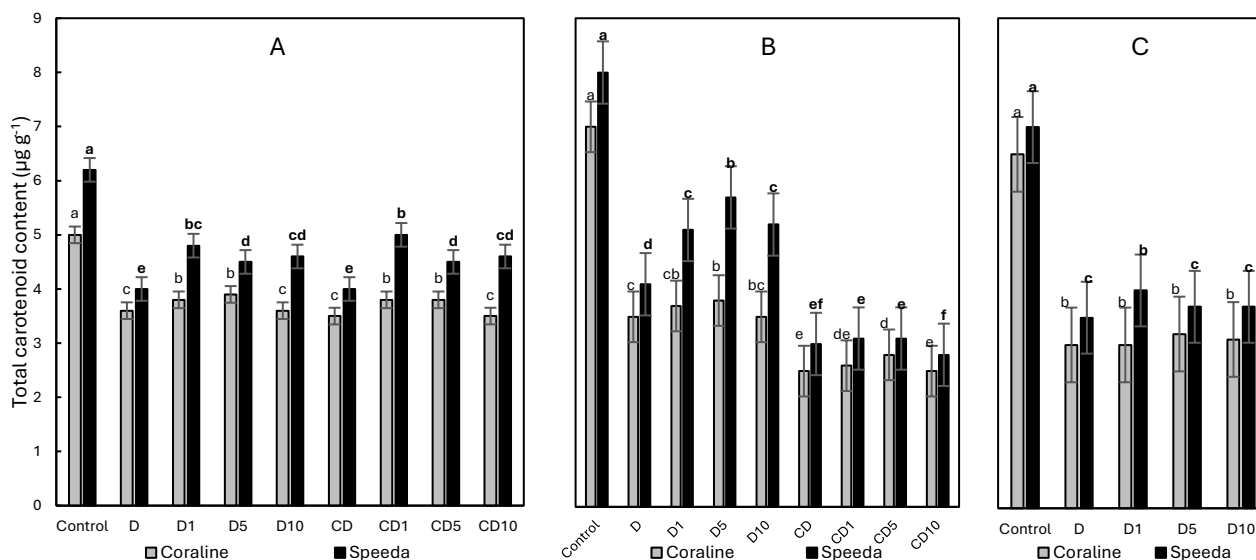


Figure 30. Total carotenoid content (µg g⁻¹) of two soybean genotypes (Coraline and Speeda) at 3 different sampling dates (A: 3 days after drought stress application at R1 stage, B: 3 days after R3 stage started, C: at the end of R4 stage) as affected by hydrogen peroxide foliar spray application under drought stress conditions (D: drought from R1 till R2 stage, D1: drought from R1 till R2 stage + 1mM hydrogen peroxide, D5: drought from R1 till R2 stage + 5mM hydrogen peroxide, D10: drought from R1 till R2 stage + 10mM hydrogen peroxide, CD: continuous drought starting from R1 stage, CD1: continuous drought starting from R1 stage + 1mM hydrogen peroxide, CD5: continuous drought starting from R1 stage + 5mM hydrogen peroxide, CD10: continuous drought starting from R1 stage + 10mM hydrogen peroxide). All values are the means of 3 replicates (columns) ± standard errors (vertical whiskers). In each genotype, different letters indicate significant differences at .05 level as indicated by Duncan's multiple range test.

Stomatal Conductance

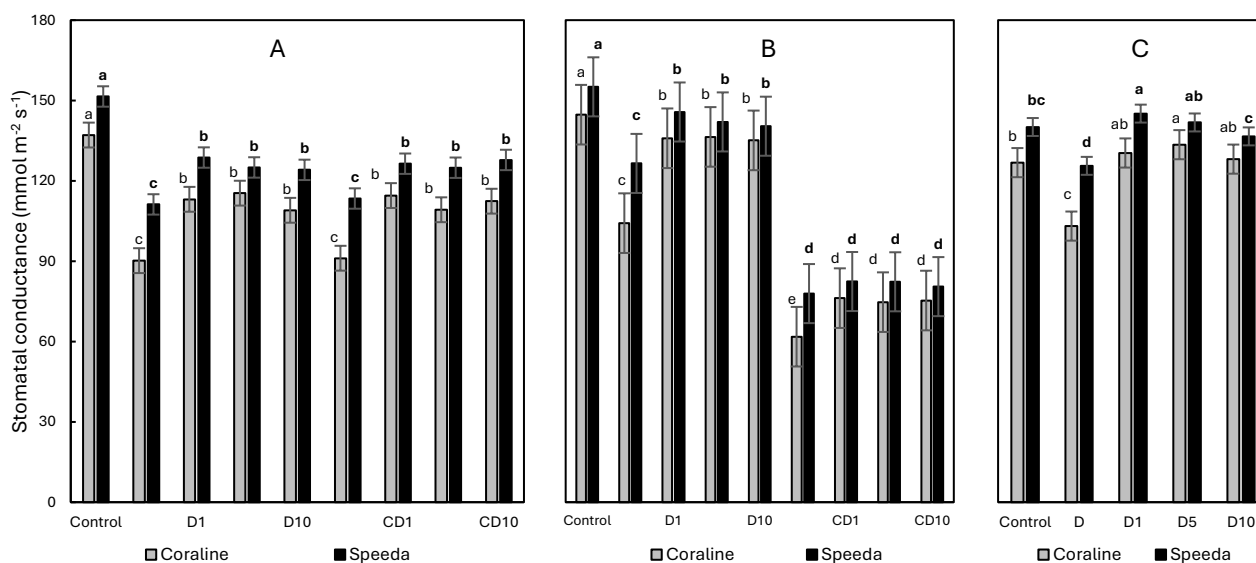


Figure 31. Stomatal conductance ($\text{mmol m}^{-2} \text{s}^{-1}$) of two soybean genotypes (Coraline and Speeda) at 3 different sampling dates (A: 3 days after drought stress application at R1 stage, B: 3 days after R3 stage started, C: at the end of R4 stage) as affected by hydrogen peroxide foliar spray application under drought stress conditions (D: drought from R1 till R2 stage, D1: drought from R1 till R2 stage + 1mM hydrogen peroxide, D5: drought from R1 till R2 stage + 5mM hydrogen peroxide, D10: drought from R1 till R2 stage + 10mM hydrogen peroxide, CD: continuous drought starting from R1 stage, CD1: continuous drought starting from R1 stage + 1mM hydrogen peroxide, CD5: continuous drought starting from R1 stage + 5mM hydrogen peroxide, CD10: continuous drought starting from R1 stage + 10mM hydrogen peroxide). All values are the means of 3 replicates (columns) $\pm$ standard errors (vertical whiskers). In each genotype, different letters indicate significant differences at .05 level as indicated by Duncan's multiple range test.

The stomatal conductance significantly decreased in both genotypes when subjected to drought stress. Similarly, Muhammad et al. (2021) and Rahman et al. (2022) reported that g_s significantly decreased in drought-stressed soybean plants. The foliar application of H_2O_2 at any concentration could significantly elevate the stomatal conductance of both Coraline and Speeda plants. The stomatal conductance of both genotypes dramatically degraded when drought stress was kept; however, the foliar spray with H_2O_2 at all concentrations could significantly increase the stomatal conductance of Coraline (by an average 22%), but not that of Speeda plants. On the other hand, the recovered plants of both genotypes had significantly higher stomatal conductance when foliar spray was applied at any concentration as compared to the recovering plants that were not sprayed. Interestingly, Coraline and Speeda plants that were sprayed with 5 mM and 1 mM H_2O_2 , respectively had significantly higher stomatal conductance values (by 5.3% and 3.7%) compared to the control counterparts that were kept under optimum conditions throughout the whole experimental period (Figure 31).

Speeda plants could maintain higher stomatal throughout the experimental period as compared to Coraline plants.

Relative water content

Sampling Date	3 days after drought stress application at R1 stage		3 days after R3 stage started		at the end of R4 stage	
Treatment	Coraline	Speeda	Coraline	Speeda	Coraline	Speeda
Control	70.5 ^a	72.0 ^a	68.9 ^a	71.0 ^a	66.6 ^a	67.4 ^{ab}
D	52.4 ^d	59.1 ^c	58.4 ^b	64.9 ^b	57.6 ^c	62.1 ^b
D1	59.4 ^c	65.6 ^b	64.2 ^a	70.1 ^a	62.2 ^b	68.7 ^a
D5	64.8 ^b	63.7 ^{bc}	65.0 ^a	65.2 ^b	63.5 ^a	64.0 ^b
D10	54.1 ^d	62.9 ^{bc}	62.3 ^b	65 ^b	60.0 ^{bc}	62.9 ^b
CD	52 ^d	59.2 ^c	40.2 ^d	49.3 ^d	NA	NA
CD1	59.5 ^c	65.3 ^b	47.6 ^c	57.7 ^c	NA	NA
CD5	65.0 ^b	63.6 ^{bc}	49.1 ^c	54.8 ^c	NA	NA
CD10	54.2 ^d	63.0 ^{bc}	47.5 ^c	53.9 ^{cd}	NA	NA

Table 1. Relative water content (%) of two soybean genotypes (Coraline and Speeda) at 3 different sampling dates as affected by hydrogen peroxide foliar spray application under drought stress conditions (D: drought from R1 till R2 stage, D1: drought from R1 till R2 stage + 1mM hydrogen peroxide, D5: drought from R1 till R2 stage + 5mM hydrogen peroxide, D10: drought from R1 till R2 stage + 10mM hydrogen peroxide, CD: continuous drought starting from R1 stage, CD1: continuous drought starting from R1 stage + 1mM hydrogen peroxide, CD5: continuous drought starting from R1 stage + 5mM hydrogen peroxide, CD10: continuous drought starting from R1 stage + 10mM hydrogen peroxide). All values are the means of 3 replicates. In each genotype, different letters indicate significant differences at .05 level as indicated by Duncan's multiple range test. NA: Not Applicable.

The relative water content of all drought-stressed treatments of both genotypes significantly decreased as compared to control treatment, regardless of H₂O₂ application and concentration. Drought stress results in reduced stomatal conductance by increasing stomatal closure ratio (Zhang et al., 2016) in order to maintain the water content of the drought-stressed plants. In their experiment, Guler and Pehlivan (2016) concluded that RWC of both experimented soybean genotypes decreased under drought stress conditions. On the other hand, the exogenous application of either 1 or 5 mM H₂O₂ on Coraline, and 1 mM H₂O₂ on Speeda significantly enhanced the RWC. After terminating drought, a very similar result was obtained, where these concentrations helped in elevating the RWC of both genotypes to reach nearly similar values to those of control plants. On the other hand, all the treatments where the plants of both genotypes were kept under drought stress conditions had significantly lower RWC, yet all treatments that received any concentration of H₂O₂ (except for 10 mM on Speeda) were able to keep significantly better RWC as compared to the non-sprayed counterpart. At the end of the podding stage, the RWC of (D1) and (D5) treatments in Coraline, and of (D1) treatment in Speeda was significantly higher than that of (D) treatment (Table 1). Previously, Ishibashi et al. (2011) and Terzi et al. (2014) reported significant enhancement in both RWC and gs in drought-stressed soybean as a consequence of H₂O₂ foliar application. At all sampling dates, the RWC of Speeda was significantly higher than that of Coraline in all drought treatments except for the D5 treatment.

Flower Number per Plant

At the end of the flowering stage, the treatments of both genotypes that were subjected to drought stress without any foliar spray produced significantly lower number of flowers (by 19.7% and 26.9% in Coraline and Speeda, respectively) as compared to control counterparts. The foliar spray enhanced this trait in Coraline, where both 1 mM and 5 mM H₂O₂ concentrations resulted in significantly higher flower number as compared to the non-sprayed treatments. However, the foliar spray did not enhance this trait in Speeda; it even decreased the flower number when 5 mM or 10 mM H₂O₂ was applied (Table 2).

Speeda had significantly higher flower numbers than Coraline in all treatments except for the treatments that were sprayed with 5 mM H₂O₂ where the flower numbers were very similar.

Treatment	Coraline	Speeda
Control	18.3 ^a	28.3 ^a
D	14.7 ^c	20.7 ^b
D1	16.3 ^b	21.3 ^b
D5	18.0 ^a	17.7 ^c
D10	14.7 ^c	17.0 ^c
CD	14.6 ^c	20.9 ^b
CD1	16.4 ^b	21.2 ^b
CD5	17.9 ^a	17.6 ^c
CD10	14.5 ^c	17.1 ^c

Table 2. Flower number of two soybean genotypes (Coraline and Speeda) at full bloom (R2) stage as affected by hydrogen peroxide foliar spray application under drought stress conditions (D: drought from R1 till R2 stage, D1: drought from R1 till R2 stage + 1mM hydrogen peroxide, D5: drought from R1 till R2 stage + 5mM hydrogen peroxide, D10: drought from R1 till R2 stage + 10mM hydrogen peroxide, CD: continuous drought starting from R1 stage, CD1: continuous drought starting from R1 stage + 1mM hydrogen peroxide, CD5: continuous drought starting from R1 stage + 5mM hydrogen peroxide, CD10: continuous drought starting from R1 stage + 10mM hydrogen peroxide). All values are the means of 3 replicates. In each genotype, different letters indicate significant differences at .05 level as indicated by Duncan's multiple range test.

Pod number per Plant

Treatment	Coraline	Speeda
Control	15.3 ^a	22.7 ^a
D	11.3 ^b	14.3 ^c
D1	14.0 ^a	17.7 ^b
D5	13.6 ^a	13.7 ^c
D10	8.3 ^c	9.7 ^d

Table 3. Pod number (plant⁻¹) of two soybean genotypes (Coraline and Speeda) at the end of R4 stage as affected by hydrogen peroxide foliar spray application under drought stress conditions (D: drought from R1 till R2 stage, D1: drought from R1 till R2 stage + 1mM hydrogen peroxide, D5: drought from R1 till R2 stage + 5mM hydrogen peroxide, D10: drought from R1 till R2 stage + 10mM hydrogen peroxide. All values are the means of 3 replicates. In each genotype, different letters indicate significant differences at .05 level as indicated by Duncan's multiple range test.

The number of pods of both genotypes decreased due to drought stress application; the reduction was more measurable and significant in Speeda (37%). The pod number significantly increased in Coraline when 1 mM or 5 mM H₂O₂ foliar spray was applied, and the same result was obtained when 1 mM H₂O₂ foliar spray was applied on Speeda (Table 3). The number of pods was higher for Speeda in all treatments as compared to Coraline.

Pod fresh weight

Significant decrease in the pod fresh weight under drought stress conditions was recorded in both genotypes. However, the application of 5 mM and 1 mM H₂O₂ foliar spray on Coraline and Speeda, respectively, has led to significant increase (by 18.1% and 14.1%, respectively) in the pod fresh weight (Table 4).

Pod fresh weight of Speeda was significantly higher than that of Coraline, regardless of drought and H₂O₂ foliar spray application.

Treatment	Coraline	Speeda
Control	19.3 ^a	34.7 ^a
D	12.7 ^c	21.3 ^c
D1	14.7 ^{bc}	24.3 ^b
D5	15.0 ^b	17.0 ^d
D10	12.7 ^c	14.7 ^e

Table 4. Pod fresh weight (g plant⁻¹) of two soybean genotypes (Coraline and Speeda) at the end of R4 stage as affected by hydrogen peroxide foliar spray application under drought stress conditions (D: drought from R1 till R2 stage, D1: drought from R1 till R2 stage + 1mM hydrogen peroxide, D5: drought from R1 till R2 stage + 5mM hydrogen peroxide, D10: drought from R1 till R2 stage + 10mM hydrogen peroxide. All values are the means of 3 replicates. In each genotype, different letters indicate significant differences at .05 level as indicated by Duncan's multiple range test.

Proline content

The leaf proline content of both genotypes significantly increased under drought stress conditions. Furthermore, the foliar application of H₂O₂ at any concentration significantly increased the leaf proline content as compared to the treatment where the drought-stressed plants were sprayed with DW. When drought was terminated, proline content measurably decreased in both genotypes, yet it was still higher than that of control treatment. Under continuous drought conditions, proline continued to accumulate, and its levels were significantly higher than those of the drought-relieved counterparts. The foliar H₂O₂ spray had no measurable effect at this point in any of the two genotypes. The leaf proline content

was still higher in the drought-relieved treatments at the end of the podding stage as compared to the control counterparts (Table 5). In their experiment, Cao et al. (2019) reported that drought-stressed soybean seedlings had 30, 125 and 334% higher proline concentration after 5, 10 and 15 days of drought stress application. Such conclusion on proline and soluble sugar accumulation was also reported on soybean by other studies (e.g., Du et al. (2020) and Iqbal et al. (2018)). It was also reported that the levels of proline accumulations are genotype-dependent and varies among the different stages of soybean development when the drought stress is taking place (Mwenye et al. 2016).

The leaf proline content was always higher in Speeda than in Coraline, and the differences were significant in all drought-stressed treatments of both groups.

Sampling Date	3 days after drought stress application at R1 stage		3 days after R3 stage started		at the end of R4 stage	
Treatment	Coraline	Speeda	Coraline	Speeda	Coraline	Speeda
Control	30.7 ^d	33.0 ^c	43.4 ^c	47.3 ^c	39.3 ^b	42.0 ^b
D	226.4 ^c	272.6 ^b	183.4 ^b	240.3 ^b	92.7 ^a	112.9 ^a
D1	253.9 ^b	391.7 ^a	142.9 ^b	166.7 ^b	81.1 ^a	100.5 ^a
D5	280.0 ^a	379.3 ^a	127.6 ^b	186.2 ^b	74.6 ^a	103.3 ^a
D10	275.8 ^{ab}	365.4 ^a	130.0 ^b	180.8 ^b	79.9 ^a	101 ^a
CD	228.3 ^c	270.6 ^b	402.7 ^a	468.1 ^a	NA	NA
CD1	255.1 ^b	390.6 ^a	449.5 ^a	521.7 ^a	NA	NA
CD5	278.4 ^a	376.0 ^a	472.8 ^a	485.5 ^a	NA	NA
CD10	275.0 ^{ab}	365.3 ^a	411.4 ^a	447.0 ^a	NA	NA

Table 5. Leaf proline content ($\mu\text{g g}^{-1}$) of two soybean genotypes (Coraline and Speeda) at 3 different sampling dates as affected by hydrogen peroxide foliar spray application under drought stress conditions (D: drought from R1 till R2 stage, D1: drought from R1 till R2 stage + 1mM hydrogen peroxide, D5: drought from R1 till R2 stage + 5mM hydrogen peroxide, D10: drought from R1 till R2 stage + 10mM hydrogen peroxide, CD: continuous drought starting from R1 stage, CD1: continuous drought starting from R1 stage + 1mM hydrogen peroxide, CD5: continuous drought starting from R1 stage + 5mM hydrogen peroxide, CD10: continuous drought starting from R1 stage + 10mM hydrogen peroxide). All values are the means of 3 replicates. In each genotype, different letters indicate significant differences at .05 level as indicated by Duncan's multiple range test. NA: Not Applicable.

Total Soluble Sugars

Drought stress significantly increased the total soluble sugars in the leaves of both genotypes. Compared to the drought-stressed treatment, the application of H_2O_2 foliar spray at any concentration in Coraline, and at 1 or 5 mM in Speeda significantly induced the accumulation of soluble sugars. When drought was eliminated after the flowering stage, the total soluble sugars in Coraline noticeably decreased and reached levels that were insignificant as compared to the control plants, whereas these levels were still significantly higher in Speeda.

Furthermore, the sprayed plants of both genotypes had very close levels of soluble sugars as compared to the non-sprayed counterparts. On the other hand, the group of treatments that had continuous drought accumulated significant levels of soluble sugars as compared to the drought-relieved group of both genotypes. In Coraline, the soluble sugar contents were not significantly different in the treatments sprayed with any concentration of H₂O₂ from the treatment that was not sprayed, whereas they were in Speeda. At the end of the podding stage, the content of the total soluble sugars was still significantly higher in the treatments that suffered from drought, regardless of H₂O₂ application and concentration, as compared to the control treatments that were sprayed with DW (Table 6). According to Khan et al. (2020), there is an important role of the elevated soluble sugar levels under drought stress conditions; that is, sustaining adequate metabolic C/N ratios.

Although Speeda plants had higher contents of the total soluble sugars, yet the differences were more announced after drought stress application, whereas these differences were much less in the group of treatments that was relieved from drought, and also at the end of the podding stage.

Sampling Date	3 days after drought stress application at R1 stage		3 days after R3 stage started		at the end of R4 stage	
Treatment	Coraline	Speeda	Coraline	Speeda	Coraline	Speeda
Control	42.5 ^c	45.9 ^d	36.1 ^b	40.2 ^d	33.3 ^b	35.8 ^b
D	123.8 ^b	165.2 ^c	65.0 ^b	84.4 ^c	51.3 ^a	59.7 ^a
D1	160.1 ^a	228.3 ^a	68.9 ^b	90.4 ^c	53.9 ^a	61.1 ^a
D5	182.7 ^a	215.8 ^{ab}	70.9 ^b	86.1 ^c	54.1 ^a	60.8 ^a
D10	173.9 ^a	195.0 ^{bc}	69.0 ^b	84.9 ^c	52.8 ^a	59.7 ^a
CD	125.0 ^b	163.9 ^c	175.3 ^a	235.7 ^b	NA	NA
CD1	162.1 ^a	230.4 ^a	184.9 ^a	286.4 ^a	NA	NA
CD5	177.7 ^a	213.8 ^{ab}	189.2 ^a	271.9 ^a	NA	NA
CD10	173.5 ^a	195.5 ^{bc}	186.6 ^a	262.8 ^a	NA	NA

Table 6. Total soluble sugars (mg g⁻¹) in the leaves of two soybean genotypes (Coraline and Speeda) at 3 different sampling dates as affected by hydrogen peroxide foliar spray application under drought stress conditions (D: drought from R1 till R2 stage, D1: drought from R1 till R2 stage + 1mM hydrogen peroxide, D5: drought from R1 till R2 stage + 5mM hydrogen peroxide, D10: drought from R1 till R2 stage + 10mM hydrogen peroxide, CD: continuous drought starting from R1 stage, CD1: continuous drought starting from R1 stage + 1mM hydrogen peroxide, CD5: continuous drought starting from R1 stage + 5mM hydrogen peroxide, CD10: continuous drought starting from R1 stage + 10mM hydrogen peroxide). All values are the means of 3 replicates. In each genotype, different letters indicate significant differences at .05 level as indicated by Duncan's multiple range test. NA: Not Applicable.

4.2.2. The Effects of Exogenous Application of Acetic Acid on The Morpho-physiology of Soybean under Severe Drought Stress Applied at Early Stages

Root Morphology

In 'Speeda', the root dry weight was not affected by the imposition of drought stress. However, the plant roots of the drought stressed treatment that received AA foliar spray had significantly lower dry weight. In 'Coraline', on the other hand, the AA foliar application resulted in significantly higher root dry weight as compared to the other treatments. The root dry weight of AA-sprayed plants (D2) was significantly higher in 'Coraline' as compared to 'Speeda', whereas it was significantly lower in both (D0) and (D1) treatments (Figure 32/A).

Both the root length and the root volume of 'Speeda' plants decreased significantly as a consequence of drought stress application. Moreover, the AA application did not have a measurable effect on any of these traits. In Corlaine, however, the foliar spray of AA significantly increased both the root length and the root volume of the drought-stressed plants (D2) as compared to the non-treated, drought-stressed counterparts (D1) (Figure 32/B and 32/C). A similar root length decrease was also reported by Sohag et al. (2020). Exogenous application of H₂O₂ on rice plants (Sohag et al. 2020) and ethanol on soybean (Rahman et al. 2021) could partially alleviate the negative effects of drought stress on root morphology. 'Speeda' had longer roots, regardless of treatment, and higher root volume in both (D0) and (D1) treatments, whereas the AA-treated (D2) treatment of 'Coraline' had significantly higher root volume as compared to (D2) treatment of 'Speeda' (Figure 32/B and 32/C).

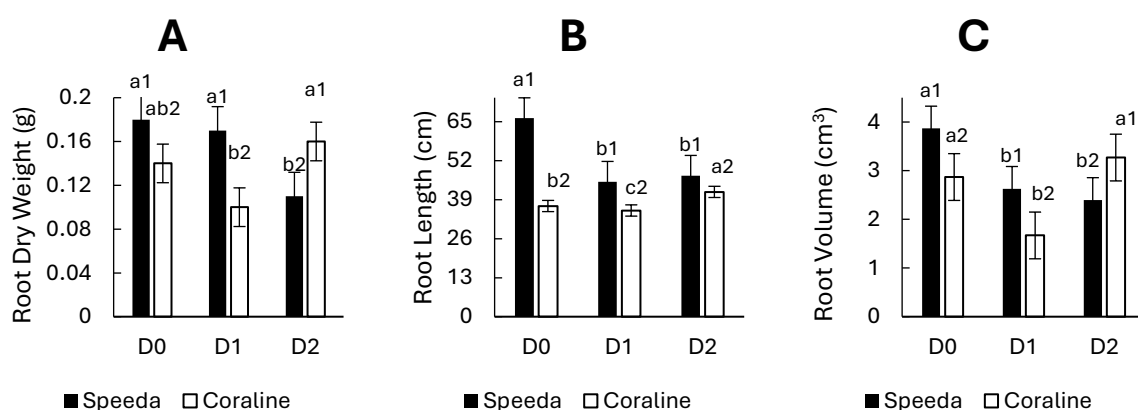


Fig 32. Root dry weight (A), root length (B) and root volume (C) of 2 soybean genotypes (Speeda and Coraline) as affected by PEG-induced drought stress and foliar acetic acid application. (D0: control, D1: drought-stressed treatment, D2: drought-stressed treatment with acetic acid spray applied). Columns represent the mean of each treatment (n = 3). Bars represent standard error (SE). Different letters indicate significant differences ($p \leq 0.05$) among treatments. Different numbers indicate significant differences ($p \leq 0.05$) between genotypes.

Shoot Morphology

Drought stress imposition significantly decreased the shoot dry weight of both genotypes. The foliar spray of AA significantly increased the shoot dry weight of 'Coraline' plants, but not of 'Speeda'. The drought-stressed (D1) 'Speeda' plants had significantly higher shoot dry weight as compared to 'Coraline' counterparts (Figure 33/A). In 'Speeda', drought stress reduced the shoot length; however, the reduction was insignificant, and the AA foliar spray did not

enhance this trait. On the contrary, drought significantly decreased the shoot length of 'Coraline' plants, and the AA application could significantly enhance this trait and keep the shoot length on a level very close to that of the control plants. 'Speeda' had higher shoot dry weight in both (D0) and (D1) treatments as compared to 'Coraline', and also higher shoot length in all treatments (Figure 33/B). Mak et al. (2014) reported that drought stress significantly decreased the shoot length of soybean plants. Garcia et al. (2010) reported the different examined soybean genotypes to be significantly different in plant height compared to one another. Ahmad et al. (2021) reported that drought reduced both shoot length and weight; however, the application of 100 mM salicylic acid increased these parameters significantly. The Authors allocated the decrease in these parameters to increased reactive oxygen species (ROS) accumulation and to changes in the proteins in the cellular walls (Boyer and Westgate 2004).

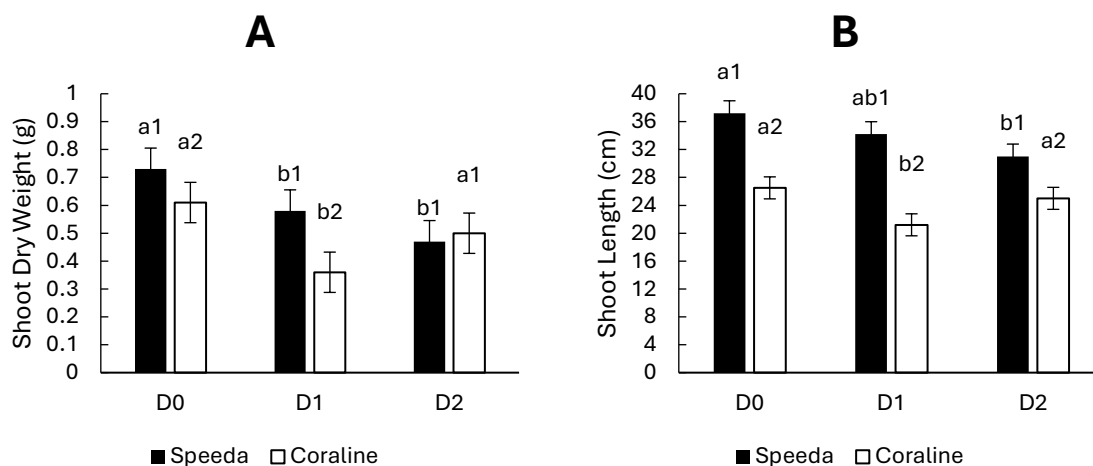


Fig 33. Shoot dry weight (A) and shoot length (B) of 2 soybean genotypes (Speeda and Coraline) as affected by PEG-induced drought stress and foliar acetic acid application. (D0: control, D1: drought-stressed treatment, D2: drought-stressed treatment with acetic acid spray applied). Columns represent the mean of each treatment (n = 3). Bars represent standard error (SE). Different letters indicate significant differences ($p \leq 0.05$) among treatments. Different numbers indicate significant differences ($p \leq 0.05$) between genotypes.

Specific Leaf Area

Drought stress imposition resulted in decreased specific leaf area (SLA) in both genotypes; however, the decrease was insignificant. The SLA significantly increased in both genotypes in drought-stressed plants sprayed with AA (D2) as compared to (D1) counterparts (Figure 34). The enhanced leaf area in (D2) treatment might be justified by promoting cell division and cell expansion as suggested by Khandaker et al. (2017) when using gibberellic acid (GA) as an exogenous foliar spray. Basal and Szabó (2020) concluded that drought stress at reproductive stages significantly decreased the leaf area of 2 soybean genotypes. Regardless of treatment, the differences between the 2 genotypes were slight and insignificant.

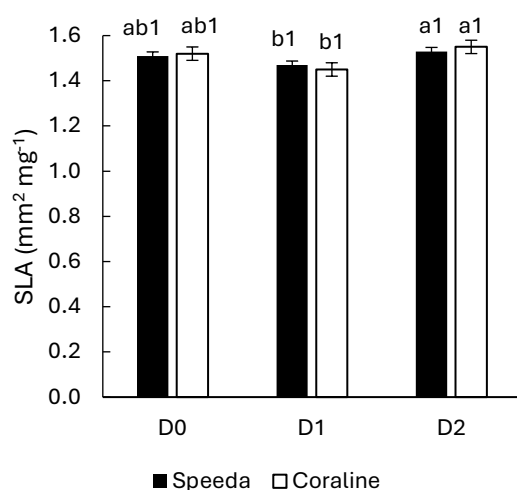


Fig 34. Specific leaf area of 2 soybean genotypes (Speeda and Coraline) as affected by PEG-induced drought stress and foliar acetic acid application. (D0: control, D1: drought-stressed treatment, D2: drought-stressed treatment with acetic acid spray applied). Columns represent the mean of each treatment (n = 3). Bars represent standard error (SE). Different letters indicate significant differences ($p \leq 0.05$) among treatments. Different numbers indicate significant differences ($p \leq 0.05$) between genotypes.

Chlorophyll Fluorescence

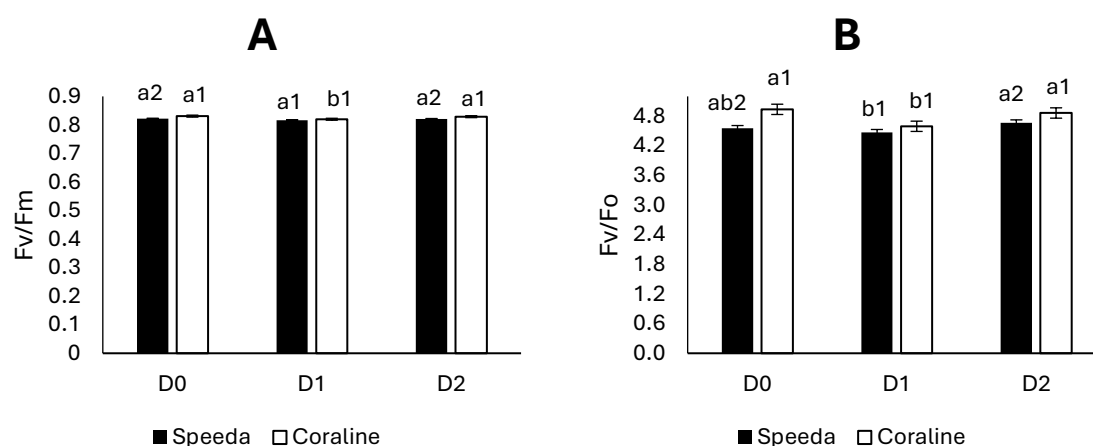


Fig 34. Optimal photochemical efficiency of PSII (Fv/Fm) (A) and the size and the number of active photosynthetic reaction centers (Fv/Fo) (B) of 2 soybean genotypes (Speeda and Coraline) as affected by PEG-induced drought stress and foliar acetic acid application. (D0: control, D1: drought-stressed treatment, D2: drought-stressed treatment with acetic acid spray applied). Columns represent the mean of each treatment (n = 3). Bars represent standard error (SE). Different letters indicate significant differences ($p \leq 0.05$) among treatments. Different numbers indicate significant differences ($p \leq 0.05$) between genotypes.

The optimal photochemical efficiency of PSII (Fv/Fm) (Figure 34/A), the size and number of active photosynthetic reaction centers (Fv/Fo) (fig. 4B) and the actual photochemical efficiency of PSII (Yield) (Figure 35) decreased in both genotypes when drought stress was imposed, with more announced effect in the case of 'Coraline'. These traits were positively influenced by the AA foliar application as their values were restored to levels very close to the control counterparts. Zlatev and Lidon (2012) reported a decrease in Fv/Fm and concluded that it can be a measure of photosynthetic down-regulation. Zhang et al. (2016) also reported

that the optimal photochemical efficiency of PSII (Fv/Fm) decreased in response to drought stress. In their experiment, Khan et al. (2023) reported that salicylic acid (SA) significantly increased both Fv/Fm and yield traits of lemongrass. This increase can be explained by the stimulatory effect of growth biostimulators such as SA on RuBisCO and brassinosteroid analogues DI-31 (Pérez-Borroto et al., 2021) on chlorophyllase enzyme activity. Earlier, Lima and Lobato (2017) indicated that growth biostimulators enhanced light absorption and electron flow, leading to higher quantum efficiency of PSII.

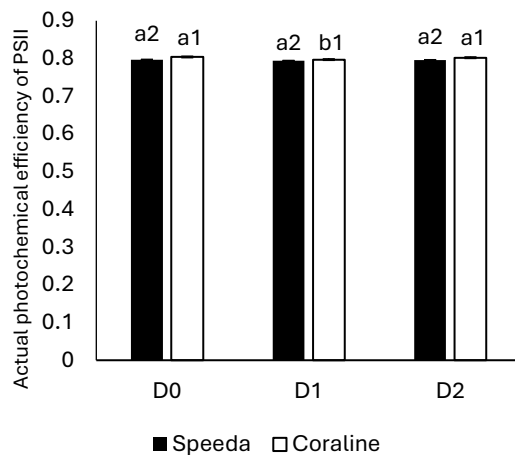


Fig 35. Actual photochemical efficiency of PSII of 2 soybean genotypes (Speeda and Coraline) as affected by PEG-induced drought stress and foliar acetic acid application. (D0: control, D1: drought-stressed treatment, D2: drought-stressed treatment with acetic acid spray applied). Columns represent the mean of each treatment (n = 3). Bars represent standard error (SE). Different letters indicate significant differences ($p \leq 0.05$) among treatments. Different numbers indicate significant differences ($p \leq 0.05$) between genotypes.

Drought stress resulted in decreased Fv/Fm value in both genotypes similarly; however, 'Coraline' plants had significantly higher Fv/Fm values under both control (D0) and AA-treated (D2) treatments (fig. 4A). Moreover, the actual photochemical efficiency was higher in 'Coraline', regardless of treatment (Figure 35).

Chlorophyll-a and chlorophyll-b contents

Chlorophyll-a level in control treatment (D0) was insignificantly higher as compared to the drought-stressed treatment (D1) in both genotypes. However, the application of AA (D2 treatment) has led to statistically significant increase in chlorophyll-a content as compared to (D1) treatment (Figure 36/A). The differences between the 2 genotypes were insignificant, regardless of treatment. It was previously reported that drought stressed plants had a substantial reduction in photosynthetic pigment concentration, but drought stressed plants treated with AA preserved the same level of photosynthetic proportionality and photosynthetic pigments throughout the drought period.

In both genotypes, drought stress did not result in measurable changes in chlorophyll-b content, however, a significant increase in this trait was recorded in (D2) treatment in both genotypes. The concentration of chlorophyll-b was higher in 'Coraline' in (D0), but lower in (D1) and (D2) treatments as compared to 'Speeda'; however, these differences were insignificant (Figure 36/B).

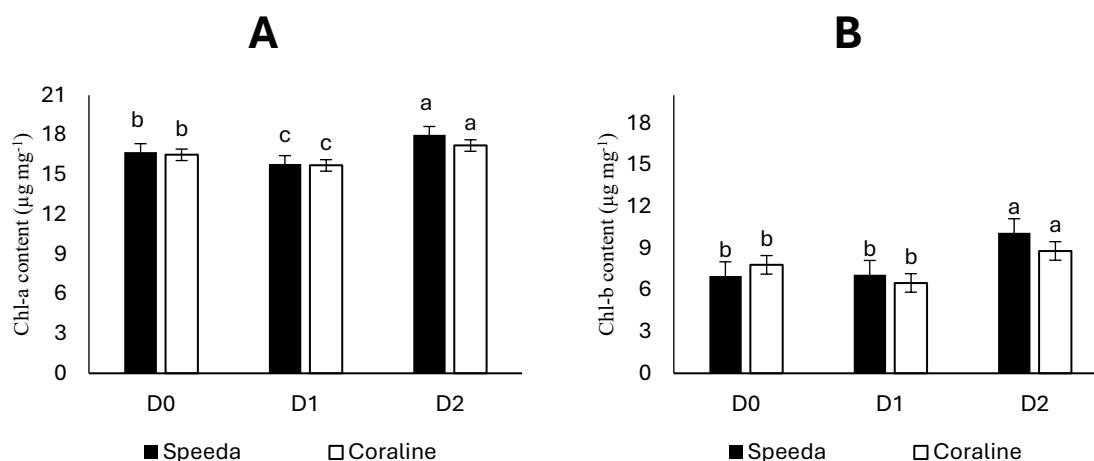


Fig 36. Chlorophyll-a content (A) and chlorophyll-b content (B) of 2 soybean genotypes (Speeda and Coraline) as affected by PEG-induced drought stress and foliar acetic acid application. (D0: control, D1: drought-stressed treatment, D2: drought-stressed treatment with acetic acid spray applied). Columns represent the mean of each treatment ($n = 3$). Bars represent standard error (SE). Different letters indicate significant differences ($p \leq 0.05$) among treatments. Different numbers indicate significant differences ($p \leq 0.05$) between genotypes.

Total Carotenoid Content

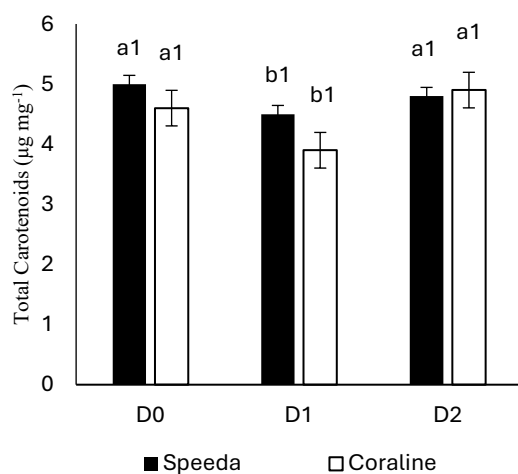


Fig 37. Total carotenoids content of 2 soybean genotypes (Speeda and Coraline) as affected by PEG-induced drought stress and foliar acetic acid application. (D0: control, D1: drought-stressed treatment, D2: drought-stressed treatment with acetic acid spray applied). Columns represent the mean of each treatment ($n = 3$). Bars represent standard error (SE). Different letters indicate significant differences ($p \leq 0.05$) among treatments. Different numbers indicate significant differences ($p \leq 0.05$) between genotypes.

Drought stress resulted in significant reduction in the total carotenoids in both genotypes. However, the drought-stressed plants that were sprayed with AA (D2) had significantly higher total carotenoids content as compared to the drought-stressed treatment (D1). Moreover, (D2) treatment resulted in total carotenoids content that was higher than the control plants in 'Coraline' genotype (Figure 37). Tang et al. (2017) found that subjecting plants to drought stress resulted in a notable decrease in carotenoid content. Low concentrations of exogenously applied growth regulators (e.g., H_2O_2 and ethanol) can induce the synthesis of

certain enzymes and/or proteins related to photosynthesis process, resulting in enhanced pigment content (Das et al. 2022). The mechanism by which these agents enhance photosynthetic pigment content (including carotenoids) is reducing the degradation rate of these pigments under drought stress conditions (Rahman et al. 2022).

Stomatal Conductance

Significant reduction in the stomatal conductance was recorded in both genotypes as a consequence of subjecting the plants to drought stress. However, the foliar application of AA enhanced this trait in both genotypes, with more pronounced effect in 'Speeda' genotype, where the increase was significant as compared to the drought-stressed counterpart (Figure 38). Drought stress (D1) reduced the stomatal conductance of both genotypes to similar levels, however, the response of 'Speeda' to foliar AA application (D2) was significantly higher than that of 'Coraline' (Figure 38). Zhang et al. (2016) discovered a 98.8 percent reduction in stomatal conductance under drought; they stated that decrease in stomatal conductance was caused by a decreased ratio of open stomata to stomatal aperture size in crops exposed to drought. According to Razmi et al. (2017), water stress decreased the stomatal conductance of three soybean leaflets as compared to their non-drought stressed counterparts, and a foliar application of 0.4 mM Salicylic Acid (SA) significantly reversed drought-induced stomatal closure and improved it.

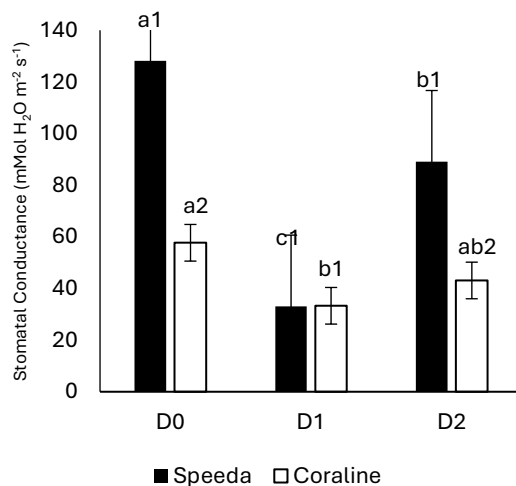


Fig 38. Stomatal conductance of 2 soybean genotypes (Speeda and Coraline) as affected by PEG-induced drought stress and foliar acetic acid application. (D0: control, D1: drought-stressed treatment, D2: drought-stressed treatment with acetic acid spray applied). Columns represent the mean of each treatment (n = 3). Bars represent standard error (SE). Different letters indicate significant differences ($p \leq 0.05$) among treatments. Different numbers indicate significant differences ($p \leq 0.05$) between genotypes.

5. Summary of Scientific Findings

- 1) Drought stress affecting soybeans during reproductive stages impairs several important morpho-physiological traits, leading to massive losses in reproductive organs and, consequently, potential yields. A post-drought recovery can still enable the plants to survive and reach maturity stages. However, the continuous severe drought occurring for longer periods during reproductive stages can lead to even complete deterioration of plants.
- 2) Negative influence of drought stress on soybean might be alleviated by the exogenous application of low concentrations of plant growth regulators (PGRs) like Hydrogen Peroxide (H_2O_2) and Acetic Acid (AA). However, the extent to which soybean plants respond is variety-dependent, and the drought-susceptible soybean varieties respond better to PGRs.
- 3) Although chickpea showed better morpho-physiology when sown in Spring, the yield of both Amorgos and Orion varieties was not affected by late sowing date when supplemental irrigation was provided, indicating that those varieties, especially Orion, which had significantly higher yield, can be sown after wheat harvesting in a sustainable cereal-legume crop rotation, allowing for less chemical N application to wheat fields.
- 4) Late sowing date significantly increased the total fat concentration in the seeds of all tested chickpea varieties under both irrigation schemes. Moreover, it significantly increased the total protein concentration in the seeds of Elmo under both irrigation schemes and in the seeds of Amorgos under supplemental irrigation scheme, whereas not affecting that of Orion.
- 5) Supplemental irrigation significantly increased the seed protein and fat concentrations in the seeds of late-sown chickpeas, amplifying the importance of such practice for enhancing chickpea seed quality.
- 6) For higher chickpea yields, supplemental irrigation of late-sown chickpea seems vital, whereas rainfed chickpeas must be sown earlier (i.e., in Spring) to achieve stable yield, although lower than irrigated counterparts.
- 7) Although Elmo chickpea variety produced comparable biomass to that of the other varieties, the seed yield was significantly lower, raising the question whether using this variety in animal feeding programs is economically feasible.
- 8) Nitrogen fertilization can significantly increase the biomass and seed yield of quinoa; however, this yield is variety dependent. Moreover, N rate should be applied after soil analysis, since higher N rates did not enhance the yield traits of both quinoa varieties tested.
- 9) Supplemental irrigation, accompanied by suitable N rate can significantly increase the yield traits of quinoa. However, N application did not seem to enhance those traits under drought stress conditions.

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7. A tézisek témakörében megjelent tudományos közlemények jegyzéke

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