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Effect of Watering Regimen on Secondary Metabolites, Physiology, and Yield of *Amaranthus cruentus*

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Abstract

Water availability is one of the most important factors that affects leafy vegetables' growth and physiological stability and accumulation of metabolites. *Amaranthus cruentus* is an economically and nutritionally valuable vegetable crop that is grown in arid and semi-arid regions. This study evaluated the comparative effect of four watering regimens; T1 (120% crop water requirement (CWR); overwatered/waterlogged), T2 (100% CWR; control/optimal), T3 (70% CWR; moderate stress), and T4 (40% CWR; severe stress); on the secondary metabolites, physiology, and growth parameters of *A. cruentus.* Optimal irrigation (T2) resulted in the maximum vegetative growth ($P < 0.05$), with the highest leaf area (870.34 cm^2), fresh shoot weight (71.23 g), dry shoot weight (9.32 g), relative water content (93.28%), chlorophyll content (2.91 mg/g FW), carotenoid content (2.91 mg/g FW), and stomatal conductance (392.34 mmol H2O $m^{-2}s^{-1}$). Secondary metabolite accumulation significantly increased when exposed to moderate drought stress (T3) with the highest accumulation of total phenolics (33.09 mg GAE/g DW), total flavonoids (22.44 mg QE/g DW) and ascorbic acid (95.34 mg/100g FW) and moderate reduction in biomass ($P < 0.05$). Severe drought stress (T4) caused maximum accumulation of proline (45.33 µmol/g FW) and increased root-to-shoot ratio (0.34), but significantly reduced stomatal conductance (38.43 mmol H2O $m^{-2}s^{-1}$), leaf area (120.11 cm^2), fresh shoot weight (13.12 g) and ascorbic acid content (20.34 mg/100g FW) ($P < 0.05$). Overwatering/waterlogging (T1) caused a decrease in the total phenolics content (11.52 mg GAE/g DW), total flavonoids content (6.41 mg QE/g DW), chlorophyll/carotenoid content (0.81 mg/g FW) and root to shoot ratio (0.06) ($P < 0.05$). In total, moderate stress (T3) will be an effective irrigation protocol to produce high levels of bioactive secondary metabolites in *A. cruentus* in a controlled manner.

Introduction

Amaranthus cruentus L. is a C_4 leafy vegetable that is a prominent crop in sub-Saharan Africa, Asia, and Latin America, and has a high nutritional value, fast growth rate, and is highly tolerant of warm temperatures. *A. cruentus* leaves have been used as a source of dietary vitamins, minerals,

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proteins and antioxidants like phenolics, flavonoids and ascorbic acid (vitamin C) (Oguji et al 2024). But water availability is becoming a constraint on the production of leafy crops in agriculture either in the form of waterlogging (Topali et al., 2024) from excess rain and/or over-irrigation, or from prolonged water stress during dry spells (Hemati et al., 2022).

Soil water levels directly influence plant physiology, water relations and biomass accumulation (Demo & Asefa 2024). Plants respond to water deficit conditions by reducing stomatal conductance to prevent water loss and consequently affecting relative water content and photosynthetic pigment retention of leaves (Asargew et al., 2024). At the same time water stress triggers biochemical changes, which results in the biosynthesis of osmoprotectants, e.g. proline to maintain turgor pressure (Khan et al., 2025). Moreover, the plants often upregulate their secondary metabolic pathways under moderate stress conditions to produce more phenolic compounds, flavonoids and antioxidant vitamins as a defence mechanism against the environmental stress (Shil & Dewanjee 2022).

In contrast, excessive watering and waterlogging cause hypoxia in the rhizosphere, affecting root respiration, stomatal opening, photosynthetic pigment degradation and nutrient and water absorption (Feng et al., 2022). It is important to determine the response of *A. cruentus* under a range of irrigation regimes that span from excess crop water requirement (CWR) (120% CWR) to severe deficit (40% CWR) to guide the development of optimized irrigation management practices aimed at achieving the highest possible yield of a bioactive compound with minimal vegetative yield.

The effect of four different watering rates (120%, 100%, 70% and 40% of the crop water requirement) on secondary metabolite content (total phenolics, total flavonoids, proline, ascorbic acid), physiological traits (relative water content, chlorophyll and carotenoid content, and stomatal conductance), and growth/yield characteristics (leaf area, leaf number, fresh shoot weight, dry shoot weight, and root to shoot ratio) in *Amaranthus cruentus* was investigated.

Materials and Methods

Experimental Design and Treatment Setup

The work was conducted in a controlled screenhouse environment in natural light. At Federal University Dutse, Jigawa State Nigeria (11.7088° N, 9.3673° E). The seeds of *A. cruentus* were collected from National Horticultural Research institute, Nihort Bagauda sub-station Kano. The seeds were sown in a propagation mixture and nursery trays. The 21-day-old seedlings were identical in uniform and the same agricultural soil was dry sieved into pots of equal volume.

The experiment was set in Randomized Complete Block Design (RCBD) and comprised four watering treatments that were based on Crop Water Requirement (CWR):

T1 (Overwatered/Waterlogged): 120% CWR, when soil moisture / waterlogging is continuously in excess.

T2 (Control/Optimal): Crop water requirement (CWR) is satisfied by 100% replacement of evapotranspirational water loss at the daily field capacity (FC) level.

T3 (Moderate Stress): 70% of crop water requirement, which is a moderate deficit irrigation.

T4 (Severe Stress): 40% of the crop water requirement which corresponds to severe water deficit conditions.

The gravimetric method was used to measure the daily pot water loss to determine the crop water requirement. The treatments were continued for 30 days after transplanting before destructive sampling and physiological analysis.

Determination of Secondary Metabolites

Determination of Total Phenolics

The Folin-Ciocalteu assay was used to determine the total phenolic content. The dried leaves sample (0.5 g) was extracted with 80% of aqueous methanol. An aliquot of the extract was mixed with Folin-Ciocalteu reagent and 7.5% sodium carbonate (Na_2CO_3) solution. The absorbance was measured at 765 nm after 30 minutes in the dark at room temperature using UV-Vis

spectrophotometer. Results were given as mg of Gallic Acid Equivalents per gram of Dry Weight (mg GAE/g DW) (Chroho et al., 2022).

Determination of Total Flavonoids

The content of total flavonoids was determined by aluminum chloride ($AlCl_3$) colorimetric method. A dried extract of the leaf was blended with 10% Aluminium chloride, 1 M potassium acetate and distilled water. The mixture was allowed to stand for 30 minutes at room temperature and absorbance was read at 415 nm. The total flavonoids content was determined by comparison with a quercetin calibration curve and reported as milligrams of quercetin equivalents per gram of dry matter (QE/g DW) (Chroho et al., 2022).

Determination of Proline Content

The acid-ninhydrin method was used to determine the free proline content. The fresh leaf tissue (0.5 g) was homogenized in 3% aqueous sulfosalicylic acid and filtered using filter paper. Equal volume of filtrate was mixed with equal volume of glacial acetic acid and acid-ninhydrin reagent and water bath for 1 hour at 100°C. Reaction was stopped in an ice bath, extraction was done with toluene and absorbance of toluene phase was measured at 520 nm. Proline concentration was determined by a standard curve and expressed as micromole of proline per gram fresh weight (μmol/g FW) (Ábrahám).

Determination of Ascorbic Acid (Vitamin C)

The ascorbic acid content was performed by titration with 2,6-dichlorophenolindophenol (DCPIP) dye method. One gram of fresh leaf tissue was homogenized in 4% oxalic acid solution and filtered. The filtrate was then titrated against a standard DCPIP dye solution until a permanent pink colour result was obtained. The concentration of ascorbic acid was determined by comparison with L-ascorbic acid solution and presented as mg/100g FW (fresh weight) (Chroho et al., 2022).

Determination of the physiological and water status parameters.

Determination of Relative Water Content (RWC)

Fresh leaf discs were used for the evaluation of Leaf relative water content (Oksana et al., 2023). The Fresh Weight (FW) of discs was recorded immediately after harvest. Then the Discs were put in distilled water in a closed Petri dish and left to stand for 4 hours at room temperature to get Turgid Weight (TW). For Dry Weight (DW) determination, the discs after recording TW were dried in a drying oven at 70°C for 48 h. RWC was calculated using the equation:

$$RWC\ (\%) = 100\ \frac{FW - DW}{TW - DW}\ X\ 100$$

Determination of Chlorophyll and Carotenoid Content

Photosynthetic pigments were extracted from fresh leaves (0.1 g) homogenized in 80% cold acetone. Homogenate was centrifuged for 10 minutes at 4000 rpm. The absorbances of the supernatant were measured at 664.1 nm, 648.6 nm, and 470 nm by spectrophotometry (Oksana et al., 2023). Total chlorophyll and carotenoid were calculated according to the formular below:

$$Chl\ a\ (\mu g/ml) = 13.36\ A_{664.1} - 5.19\ A_{648.6}$$

$$Chl\ b\ (\mu g/ml) = 27.43\ A_{648.6} - 8.12\ A_{664.1}$$

$$Car\ (\mu g/ml) = ((1000A_{470} - 2.13a - 97.64b))/209$$

Determination of Stomatal Conductance

Stomatal conductance (gs) was measured between 09:00 AM and 12:00 PM under clear skies using a portable steady-state leaf porometer. Measurements were taken on fully expanded, sun-lit leaves of uniform developmental age from the upper third canopy of the *Amaranthus cruentus* plants. A total of **3** representative plants were sampled per treatment group across all replicates**.** The porometer was calibrated for humidity and temperature prior to use. The sensor clip was secured onto the leaf blade, avoiding the midrib and ensuring a tight seal against ambient air. Once the diffusion gradient equilibrated (30 to 45 seconds), the stable value was recorded in millimoles per square meter per second (mmol m^{-2} s^{-1}).The recorded stomatal conductance values were compiled and expressed as mean values ± standard error (SE) for each watering regimen.

Determination of Growth & Yield Parameters

Determination of Leaf Area and Leaf Number

The number of leaves per plant was determined by counting the number of fully expanded leaves. Leaf area was measured with a leaf area meter and recorded as square centimetre (cm^2).

Determination of Fresh and Dry Shoot Weight

Shoots were cut at the soil interface and weighed on an analytical balance for Fresh shoot weight (g). These were then put in a paper bag and oven dried at 70°C until a constant weight for Dry Shoot Weight (g) was recorded.

Determination of Root-to-Shoot Ratio

Dry root weight was determined after careful washing of roots to remove soil particles and oven drying them at 70°C to constant weight. Root-to-Shoot Ratio was determined as a ratio of the following formula:

$$\text{Root-to-Shoot Ratio} = \frac{\text{Dry Root Weight (g)}}{\text{Dry Shoot Weight (g)}}$$

Statistical Analysis

One-way Analysis of Variance (ANOVA) was used to analyse the data. Post-hoc tests were used to compare the treatment means at a significance level of $P < 0.05$. Data is given as Mean ± SD.

Results and Discussion

Results

Effect of Watering Regimen on the Secondary Metabolites of *A. cruentus*

Watering regimens had a significant impact on the secondary metabolite profile of *Amaranthus cruentus* (Table 1).

The moderate drought stress (T3) showed maximum levels of total phenolics (33.09 mg GAE/g DW) and total flavonoids (22.44 mg QE/g DW). There was a 2.48-fold higher phenolics and a 2.66-fold higher flavonoids compared to T2 control plants. Highest phenolics and flavonoids were found in the plants grown in the wettest conditions (T2: 20.44 mg GAE/g DW and 18.13 mg QE/g DW) and lowest in the plants growing under severe stress (T4: 22.21 mg GAE/g DW and 14.23 mg QE/g DW) whereas the lowest phenolics and flavonoids were observed in the waterlogged plants (T1: 11.52 mg GAE/g DW and 6.41 mg QE/g DW).

The ascorbic acid (vitamin C) was also found to be high in T3 (moderate stress) with a value of 95.34 mg/100g FW whereas in T2 (moderate stress) it was 79.23 mg/100g FW. The severe stress (T4) caused a significant decrease in ascorbic acid content to 20.34 mg/100g FW and overwatering (T1) caused a significant decrease of ascorbic acid content to 34.37 mg/100g FW. In contrast, there was direct positive relationship between drought severity and proline accumulation in the free form with its lowest occurrence in T2 control and highest in severe drought (T4) with value of 1.9 and 45.33 µmol/g FW respectively. The lowest proline level (1.50 µmol/g FW) was observed in waterlogged plants (T1) ($P < 0.05$).

Effect of Watering Regimen on the Physiology of *A. cruentus*

There were significant differences in physiological responses between watering treatments (Table 2).

The control plants with high watering (T2) had the highest Leaf Relative Water Content (RWC) of 93.28% ($P < 0.05$). The moderate stress (T3) and waterlogging (T1) caused similar reductions in leaf hydration (74.45% and 75.54%, respectively) but severe drought (T4) caused a significant decrease in RWC to 48.56%.

The optimal irrigation (T2: 2.91 mg/g FW) had the highest amount of photosynthetic pigments (chlorophyll and carotenoids) ($P < 0.05$). Content of pigments was reduced in T3 (1.91 mg/g FW), T4 (1.33 mg/g FW) and lowest in overwatered T1 plants (0.81 mg/g FW).

The stomatal conductance (gs) was highest in the T2 (392.34 mmol H2O $m^{-2}s^{-1}$). Stomatal restriction was found in moderate stress (T3: 152.23 mmol H_2O $m^{-2}s^{-1}$), overwatering (T1: 80.56 mmol H_2O $m^{-2}s^{-1}$) and severe drought stress (T4: 38.43 mmol H_2O $m^{-2}s^{-1}$) ($P < 0.05$).

Effect of Watering Regimen on the Growth and Yield of *A. cruentus*

Irrigation supply significantly influenced morphological growth parameters as well as biomass allocation (Table 3).

Table 1: Effect of watering regimen on Secondary Metabolites of *Amaranthus cruentus*

Parameter	Unit	T1: Waterlogged (120%)	T2: Optimal / Control (100%)	T3: Moderate Stress (70%)	T4: Severe Stress (40%)
Total Phenolics	mg GAE/g DW	11.52 ± 0.03^{c}	13.33 ± 0.12^{c}	33.09 ± 0.91^{a}	22.21 ± 0.23^{b}
Total Flavonoids	mg QE/g DW	6.41 ± 0.02^{cd}	8.45 ± 0.28^{c}	22.44 ± 1.22^{a}	14.23 ± 0.03^{b}
Proline Content	µmol/g FW	1.50 ± 0.01^{c}	1.9 ± 0.02^{c}	9.32 ± 1.11^{b}	45.33 ± 0.12^{a}
Ascorbic Acid (Vit C)	mg/100g FW	34.37 ± 0.91^{c}	79.23 ± 1.12^{b}	95.34 ± 1.32^{a}	20.34 ± 1.65^{d}

Different small letters indicate significant differences among the watering treatments ($P < 0.05$)

Table 2: Effect of watering regimen on Physiology of *Amaranthus cruentus*

Parameter	Unit	T1: Waterlogged (120%)	T2: Optimal / Control (100%)	T3: Moderate Stress (70%)	T4: Severe Stress (40%)
Relative Water Content	%	75.54 ± 2.11^{b}	93.28 ± 2.45^{a}	74.45 ± 2.18^{b}	48.56 ± 2.53^{c}
Chlorophyll & Carotenoids	mg/g FW	0.81 ± 0.03^{b}	2.91 ± 0.32^{a}	1.91 ± 0.02^{b}	1.33 ± 0.01^{b}
Stomatal Conductance	mmol $H2O\ m^{-2}s^{-1}$	80.56 ± 1.45^{c}	392.34 ± 8.43^{a}	152.23 ± 4.22^{b}	38.43 ± 1.39^{d}

Different small letters indicate significant differences among the watering treatments ($P < 0.05$)

Table 3: Effect of watering regimen on Growth & Yield of *Amaranthus cruentus*

Parameter	Unit	T1: Waterlogged (120%)	T2: Optimal / Control (100%)	T3: Moderate Stress (70%)	T4: Severe Stress (40%)
Leaf Area	cm^2	159.45 ± 8.98^{c}	870.34 ± 20.37^{a}	440.89 ± 10.34^{b}	120.11 ± 8.63^{c}
Fresh Shoot Weight	G	15.23 ± 1.01^{c}	71.23 ± 2.11^{a}	45.48 ± 0.34^{b}	13.12 ± 1.21^{c}
Dry Shoot Weight	G	2.21 ± 0.03^{b}	9.32 ± 1.21^{a}	7.32 ± 0.91^{a}	1.51 ± 0.08^{b}
Root-to-Shoot Ratio	Calculated Fraction	0.06 ± 0.01^{b}	0.12 ± 0.45^{b}	0.23 ± 0.02^{a}	0.34 ± 0.01^{a}

Different small letters indicate significant differences among the watering treatments ($P < 0.05$)

The maximum leaf area expansion (870.34 cm^2), fresh shoot yield (71.23 g) and dry shoot yield (9.32 g) were obtained for optimal irrigation (T2) ($P < 0.05$). Under moderate stress (T3), leaf area, fresh shoot weight and dry shoot weight were reduced to 440.89 cm^2, 45.48 g and 7.32 g respectively. Under severe drought (T4), no significant difference was observed in leaf area, fresh shoot weight, and dry shoot weight (120.11cm^2, 13.12g, 1.51g, respectively). Similarly, overwatered plants (T1) had growth suppression (159.45 cm^2 leaf area, 15.23 g fresh shoot weight, 2.21 g dry shoot weight). The root-to-shoot ratio also rose as water stress was increased, from 0.06 with overwatered T1 to 0.12 with control T2 to 0.23 with T3 and 0.34 with T4 (severe drought).

Discussion

The non-linear response of secondary metabolites at various watering regimens illustrates abiotic stress elicitation effect in moderate water deficit.

Under moderate stress (T3), peak concentrations of total phenolics (33.09 mg GAE/g DW), total flavonoids (22.44 mg QE/g DW) and ascorbic acid (95.34 mg/100g FW) were found, suggesting that 70% crop water requirement is a stimulus for the accumulation of secondary metabolites in *A. cruentus*. Under controlled water deficit, plants increase the biosynthesis of phenylpropanoids to cope with the production of reactive oxygen species (ROS) caused by changes in energy dissipated in light reactions (Ninkuu et al., 2025). Likewise, the production of ascorbic acid also rises to maintain the redox balance of cells in response to T3.

Under extreme drought stress (T4), however, the accumulation of secondary metabolites was reduced as compared to T3 (phenolics decreased to 22.21 mg GAE/g DW, ascorbic acid decreased to 20.34 mg/100g FW). A decrease in this reduction means that enzymes protein machinery is damaged by extreme desiccation and availability of photosynthate is reduced which is essential for the synthesis of secondary products (Zahra et al., 2023). Waterlogging (T1) led to the lowest levels of secondary metabolites due to the hypoxia of the root zone which reduces root metabolic activity and the secondary pathways (Feng et al., 2022).

Leaf physiology parameters are associated with different adaptation strategies in the different soil moisture regimes. The difference between T2 (392.34 mmol H_2O $m^{-2}s^{-1}$) and T3 (152.23 mmol H_2O $m^{-2}s^{-1}$) and T4 (38.43 mmol H_2O $m^{-2}s^{-1}$) shows that the stomatal closure mechanism was working to reduce transpiration loss during water deficits. Hypoxia in waterlogged plants, combined with reduced hydraulic root signal conduction (Feng et al., 2022), is responsible for stomatal restriction (80.56 mmol H_2O $m^{-2}s^{-1}$) in T1 plants.

Under water deficits, proline accumulation is a protective osmolyte (Khan et al., 2025). The large proline pool in T4 (45.33 μmol/g FW, a 23.8 fold greater than control plants) indicates its involvement in the osmotic adjustment and maintenance of turgor in the cells under severe moisture stress. The decrease in total chlorophyll and carotenoids under drought (T3 and T4) and waterlogging (T1) is attributed to degradation of pigments under stress and chlorosis (Munné-Bosch 2025).

The morphological parameters indicate that there is the need for the optimal water supply (T2) for maximum vegetative growth and fresh shoot yield (71.23 g). Under drought stress, plants will have lower stomatal aperture leading to lower photosynthetic rates (Zahra et al., 2023), and reduced leaf expansion and shoot biomass due to lower turgor pressure.

As the root-to-shoot ratio increased with each generation from T1 (0.06) to T4 (0.34), it shows a functional biomass re-allocation strategy. In water-limited environments plants tend to invest more assimilate in the roots than in shoot dry matter in order to tap into deeper soil resources for water (Yan et al., 2023). Waterlogged T1 plants exhibited a very small root to shoot ratio (0.06), indicating hypoxic soil conditions that inhibit and cause root decay (Topali et al., 2024).

Conclusion

This research demonstrates that secondary metabolite profile, gas exchange physiology and biomass allocation of *Amaranthus cruentus* is significantly affected by irrigation regimens. Optimal irrigation (100% CWR) results in the highest vegetative yield, the highest leaf area and the lowest basal concentration of bioactive compounds, with the highest photosynthetic pigment retention. Moderate level of drought stress (70% CWR) is the most effective elicitor inducing the maximum accumulation of total phenolics, total flavonoids and ascorbic acid with moderate shoot biomass. Severe drought (40% CWR) induces a high production of proline and root allocation and it greatly reduces yield and ascorbic acid content. Overwatering or Water logging (120% CWR) causes reduction in growth as well as phytochemicals. The study suggests that irrigation at 70% CWR is a good management option for improving the nutraceutical quality of *A. cruentus* without incurring significant biomass penalties.

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Author contributions

"A.A" conceived and designed the study. "M.M" performed the experiments, collected the data, and wrote the initial draft of the manuscript. All the authors reviewed, edited, and approved the final version of the manuscript.

Conflict of Interest

The authors declare no conflict of interest

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