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ORIGINAL PAPER

Seed Priming Enhances Germination and Morphological, Physio-Biochemical, and Yield Traits of Cucumber under Water-Deficit Stress

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Abstract

Purpose Growth and productivity of high-value crops, such as cucumber (*Cucumis sativus* L.), are seriously threatened by irrigation water scarcity necessitating the adoption of climate-friendly drought mitigation practices. Seed priming has a proven role in enhancing seed germination, early seedling growth, reproductive development, and yield attributes under stressed conditions. The objective of this study was to assess the comparative effectiveness of different priming materials on morphological parameters, physio-biochemical traits, fruit yield, and irrigation water productivity of cucumber under water-deficit stress.

Methodology A factorial polyhouse experiment consisting of two factors, six priming treatments (non-primed control, hydropriming, and priming with potassium nitrate [KNO_3], dipotassium phosphate [K_2HPO_4], gibberellic acid [GA_3], and salicylic acid [SA]) and four soil moisture regimes (40%, 60%, 80%, and 100% field capacity [FC]), was conducted.

Results Decreasing soil moisture level from 100 to 40% FC caused a 37–48% reduction in shoot dry matter, 30–51% reduction in fruit weight, 77–84% reduction in fruit yield, 41–48% reduction in membrane stability index, and 30–119% increase in electrolyte leakage across seed priming treatments. Seed priming improved all evaluated germination, morphological, fruit yield and quality, and physio-biochemical traits, where KNO_3 was the most effective priming material, which caused more than three-fold increase in fruit yield and irrigation water productivity compared with the non-primed plants. Physio-biochemical performance in terms of free proline concentration, net photosynthetic rate, stomatal conductance, and transpiration rate was also enhanced in the KNO_3-primed plants in comparison to the non-primed plants regardless of soil moisture regimes.

Conclusion The results imply that priming of cucumber seeds, especially with KNO_3, protects plants against water loss and increases their dehydration tolerance. Seed priming with KNO_3 could be recommended for cucumber production under limited soil moisture availability.

Keywords Abiotic stress · *Cucumis sativus* L. · Drought stress · Photosynthesis · Water productivity

1 Introduction

For the last few decades, the supply and availability of food have increased around the world largely due to changes in agricultural practice. These increased supply and availability of food have been realized through productivity gain, greater food diversity, less seasonal dependence, rising income levels, and falling food prices (Kearney 2010). However, safe and quality fruits, vegetables, and animal feed production lag substantially behind the level required to meet nutritional requirements, which would be a critical issue in the near future among all stakeholders within the supply chain (Leisner 2020). Achieving food and nutrition security is a multidimensional issue, where agriculture plays the leading

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role (Mc Carthy et al. 2018). Freshwater scarcity, declining soil fertility, and climate change further exacerbate threats to food production systems (Foley et al. 2011). According to the recently projected climate change scenarios, the severity and frequency of drought will aggravate. Nevertheless, competition for the limited amount of freshwater available for irrigation (water for agriculture, or growing crops) is increasing, and at the same time the industrial sector and municipal water suppliers strive to satisfy the needs of an ever-growing consumer population (Egilla et al. 2001). Because freshwater available for agricultural activities is already getting scarce, groundwater extraction is unavoidable during a drought period (Leskovar and Piccinni 2005). Any shortage of the required amount of irrigation water, especially during the critical crop growth stage, can cause severe yield reduction even if all other required nutrients remain in optimum amount (Nair et al. 2008). Plants morpho-physiological characters accompanied by metabolism are altered (such as closure of stomata, dehydration of cellular structure, and reduction of antioxidant capacity) when they are exposed to water shortage at any phase of growth and development (Ashraf et al. 2011; Chen et al. 2019). In addition, leaf relative water content (LRWC), net photosynthetic rate (P_n), stomatal regulation (g_s), and transpiration rate (E) are adversely affected by water-deficit stress (Tuna et al. 2010). Consequently, plants synthesize a variety of enzymatic (superoxide dismutase, peroxidase, glutathione reductase, catalase, ascorbate peroxidase, and mono-dehydroascorbate reductase) and non-enzymatic (carotenoids, anthocyanins, phenolics, glycinebetaine, proline, phenols, flavonoids, and ascorbic acid) antioxidants to detoxify drought stress-induced generation of reactive oxygen species (ROS) (Kosar et al. 2015).

Seed priming is amongst the most cost-effective and practical approaches that leads to effective germination. This, in turn, improves the initial seedling growth and results in high yield production with better quality, especially under environmental stresses (Nakaune et al. 2012). It is the simplest technique to ensure a rapid, uniform, and efficient seed germination, emergence, and establishment, which makes the seedlings become more resilient to subsequent environmental stresses (Farooq et al. 2019, 2021; Alam et al. 2022; Das et al. 2022). Seed priming approaches are usually classified into various types based on the priming material used, namely hydropriming, chemopriming, hormonepriming, biopriming, osmopriming, nutriopriming, solid matrix priming, and thermopriming (Mitra et al. 2021). In cantaloupe (*Cucumis melo* L.), pre-sowing salicylic acid (SA) seed priming treatment has been shown to enhance seed germination, early seedling growth, and crop productivity under water-deficit stress (Alam et al. 2022). Halopriming cucumber (*Cucumis sativus* L.) seeds with potassium dihydrogen phosphate (KH_2PO_4) and dipotassium hydrogen orthophosphate/dipotassium phosphate (K_2HPO_4) have been reported to improve seed germination and vigor compared with the non-primed seeds (Pandey et al. 2017). An improvement in cucumber seedling growth, fresh and dry weight, total chlorophyll content, photosynthetic activity, and leaf nutrient content has been observed with gibberellic acid (GA_3) and potassium nitrate (KNO_3) seed priming (Anwar et al. 2020). Metabolic activities (including an enhancement of antioxidant activity and repairing processes) for germination start faster in primed seed, endosperm imbibition faces less physical resistance, and cell membrane renovates with an immature embryo, but the development of radicle is prohibited (Kubala et al. 2015). Priming-induced accelerated stress tolerance has been attributed to: (i) an increased expression of various stress-related genes and proteins, (ii) an enhanced protection to the cellular proteins damaged through natural aging, and (iii) an increased production of free radical scavenging enzymes, which protect the cell against membrane damage due to lipid peroxidation (Varier et al. 2010; Nakaune et al. 2012). Additional advantages include greater synthesis and activation of enzymes catalyzing the breakdown and mobilization of storage reserves, adequate post-germination nutrient uptake and energy/water conservation, higher capacity to circumvent thermodormancy, proper maturation, and more agricultural production (Sung et al. 2008; Varier et al. 2010; Nakaune et al. 2012). However, numerous factors influence the performance of seed priming, including plant species, priming material, priming duration, priming media concentration, environmental conditions, and shelf-life conditions. Seeds that have been treated with the appropriate priming material germinate better, for example, osmotic priming with polyethylene glycol (PEG 8000) has been reported to improve germination performance, seed reserve utilization, early seedling growth, and antioxidant defense system, which confer better drought tolerance in sorghum [*Sorghum bicolor* (L.) Moench] (Tounekti et al. 2020).

Cucumber, a popular vegetable crop of economic importance, is widely cultivated under greenhouse and open-field conditions and is consumed across the globe due to its high nutritional value (Anwar et al. 2020). It is a rich source of minerals, vitamins, and antioxidants (Patel and Panigrahi 2019). However, the growth and development of cucumber plants are highly susceptible to soil moisture depletion as the plants have shallow root systems with around 85% of the root length confined in the top 30 cm of soil (Janoudi and Widders 1993). Like other Cucurbits, cucumber has a high transpiration rate and requires high soil moisture during its lifetime; therefore, drought stress is a limiting factor for its growth and fruit yield (Wang et al. 2012). Although several researchers have evaluated the beneficial role of a range of priming materials on growth, physiology, and fruit yield of cucumber, a comparison among these priming materials under various soil moisture regimes has not

been adequately made. It was hypothesized that cucumber plants would respond differently to different priming materials in terms of vegetative growth, fruit yield and quality, and physio-biochemical attributes under different soil moisture levels. The objective of the present study was to evaluate the comparative effectiveness of different priming materials on growth, physio-biochemical traits, fruit yield, and irrigation water productivity of cucumber under water-deficit stress.

2 Materials and Methods

2.1 Germination Trial

Prior to conducting the polyhouse experiment, a germination test was performed in the laboratory. The surface of cucumber seeds (var. Pretty, Advance Seed Co., Ltd., Pathum Thani, Thailand) was disinfected with 3% H_2O_2 for 10 min and then gently washed three times with distilled water. The germination test was carried out on samples of 20 seeds per Petri dish; when the seed coat was ruptured and the radicle was visible, it was rated as germinated. Six priming treatments were prepared for the disinfected seeds: non-primed control (dry seeds without prior presoaking), hydropriming (dry seeds soaked in distilled water), and priming with KNO_3 (5%, w/v), K_2HPO_4 (1%, w/v), GA_3 (0.02%, w/v), and SA (0.005%, w/v) each dissolved in 100 mL of distilled water. The seeds were then placed on 10 cm diameter Petri dishes with two layers of Whatman #1 filter paper and kept in the laboratory at room temperature (25 ± 2 ºC). Seed germination was monitored daily for 7 days after the initiation of the experiment and deionized water was added according to the requirement. Petri dishes were arranged following a completely randomized design, and each treatment was replicated four times.

Seeds having a minimum emergent radicle length of 2 mm were considered to be germinated (Alsaeedi et al. 2018). Germination percentage and germination rate were determined using the following formulae as outlined by Biju et al. (2017) and Alam et al. (2022):

$$\text{Germination percentage } (\%) = \frac{\mathrm{n}}{\mathrm{N}} \times 100$$

where n is the number of germinated seeds and N is the total number of seeds.

$$\text{Germination rate (seed day}^{-1}) = \sum_{\mathrm{i}=1}^{\mathrm{k}} \frac{\mathrm{n_i}}{\mathrm{t_i}}$$

where n_i is the percentage of seeds germinating on the i_{th} day and t_i is the number of days counted from the start of the experiment (i) to k, the last day on which seeds germinated.

Germination energy was computed using the following formula as suggested by Hernández-Herrera et al. (2014) and Alam et al. (2022).

$$\text{Germination energy } (\%) = \frac{\text{Number of germinating seeds}}{\text{Number of total seeds per treatment after germination for three days}} \times 100$$

Mean germination time was calculated using the following formula as outlined by Ellis and Roberts (1981) and Alam et al. (2022).

$$\text{Mean germination time (day)} = \sum \frac{\mathrm{n} \times \mathrm{d}}{\mathrm{N}}$$

where n is the number of seeds germinated on each day, d is the number of days from the beginning of the trial, and N is the total number of seeds germinated at the termination of the trial.

3 Polyhouse Experiment

3.1 Experimental Setup

The experiment was carried out in a polyhouse at the Asian Institute of Technology's Department of Food, Agriculture, and Bioresources (latitude 14°04′53" N and longitude 100°36′33" E), Klong Luang, Pathum Thani, Thailand, from December 2021 to February 2022. Plants were grown in a naturally-lit polyhouse with a relative humidity of 70–75% and a temperature of 30–35 °C. The soil, known as Bangkok clay soil, was collected from the top layer (0–20 cm depth) of the research farm. The soil contains 22% sand, 17% silt, 61% clay, 2.5% organic matter, and a pH of 5.2 (1:1 water). The soil is characterized by 5000 mg kg^{-1} total N, 44 mg kg^{-1} available P, 304 mg kg^{-1} exchangeable K, and 3300 mg kg^{-1} exchangeable Ca. After separating undesired materials (coarse fragments, stones, pebbles, plant roots, and debris), the soil was sun-dried for 5 days before being crushed into small pieces and finally placed into plastic pots (15 kg soil per pot) with the dimension of 30 cm (height) × 36 cm (top diameter) × 28 cm (bottom diameter). Plants were fertilized with the recommended fertilizer dose for cucumber cultivation by the Department of Agriculture, Royal Thai Government. Accordingly, NPK 15:15:15 at 124 kg ha^{-1} as a basal dose, urea 46:0:0 at 186 kg ha^{-1} as a top dress at 7 days after germination, and NPK 15:15:15

at 124 kg ha^{-1} as a top dress at the flowering stage were applied. Flowers were manually pollinated in all plants. All plants were individually tied using vertically positioned nylon ropes and kept in an upright position throughout the growing period.

3.1.1 Experimental Design and Treatment

The experiment was setup in a completely randomized design with factorial combination of six priming materials and four water regimes. There were four replications of each treatment combination. The first factor consisted of six priming materials: non-primed control, hydropriming, and priming with KNO_3 (5%, w/v), K_2HPO_4 (1%, w/v), GA_3 (0.02%, w/v), and SA (0.005%, w/v) each dissolved in 100 mL of distilled water. Seed priming materials and doses were selected based on Piri et al. (2009), Rehman et al. (2011), Anwar et al. (2020), and Alam et al. (2022). The second factor comprised of four soil moisture regimes (40%, 60%, 80%, and 100% field capacity [FC]). The soil moisture regimes were selected based on Parkash et al. (2021). Soil moisture contents at 40%, 60%, 80%, and 100% FC were determined as 19%, 28%, 37%, and 46%, respectively, using a modified methodology as described by Datta et al. (2009).

Cucumber seeds (var. Pretty) were immersed into four chemical solutions for 24 h at room temperature (25 ± 2 °C) with a seed weight to priming solution volume ratio of 1:5 (w/v). All the seeds were then thoroughly rinsed three times in distilled water, followed by the removal of surface water using blotting paper and a 2-day drying in the shade at room temperature. The non-primed control consisted of dry seeds without any presoaking. Seeds were submerged in distilled water at room temperature for 24 h, kept in the dark, and then dried using blotting paper for the hydropriming treatment. For germination, seeds were placed in compact trays using sterile peat moss as a substrate on 04 December 2021. At the two-true leaf stage, one healthy and vigorous seedling (15-day-old) was transplanted into each pot, which was regarded as one treatment combination. Healthy and vigorous seedlings were initially selected from each priming treatment to make sure that later differences in response of different plants could be attributed to the imposed drought stress rather than their inherent poor/strong vigor. To ensure proper seedling establishment and overcome transplanting shock, all pots were irrigated with the same amount of water for the initial 2 weeks. After that, four predetermined soil moisture regimes were imposed in the respective pots at 40%, 60%, 80%, and 100% FC as defined in the experimental design. The desired soil moisture regimes were maintained by withholding irrigation until the soil moisture level dropped below the desired level, followed by irrigation to the extent that the soil moisture corresponded to the desired level. Throughout the crop growth period, a handheld soil moisture meter (SM150 Soil Moisture Sensor; SM150, Delta-T Devices Ltd., Cambridge, UK) was utilized to monitor soil moisture on a daily basis.

3.1.2 Data Collection

At harvest, data on plant growth (plant height, number of leaves per plant, shoot dry matter, and root dry matter), fruit yield parameters (number of fruits per plant, fruit length, fruit diameter, fruit weight, and fruit yield), irrigation water productivity, and fruit quality (total soluble solids [TSS]) were collected. Data on reproductive parameters (days to flowering, days to fruit set, and days to fruit maturity) were recorded after the vegetative growth period. Four weeks after implementing the desired soil moisture levels, data on physio-biochemical parameters, such as leaf greenness (SPAD value), LRWC, electrolyte leakage, membrane stability index, P_n, g_s, E, and free proline concentration were collected.

Morphological and reproductive parameters Plant height (cm) was measured using a meter scale from the surface of the soil to the plant tip, and the number of leaves per plant was manually counted. Following fruit harvest, shoot and root biomass samples were collected, and dry weights were measured after oven drying at 72 °C until a constant weight was achieved. Data on days to flowering, days to fruit set, and days to fruit maturity were recorded by regular visual assessment.

Fruit yield parameters, fruit yield, fruit quality, and irrigation water productivity Number of fruits per plant was manually counted after fruit harvest. A vernier caliper was used to measure fruit length (cm) and fruit diameter (cm). Fruits from each plant were weighed using an electronic balance and referred to as fruit yield (g $plant^{-1}$). A digital refractometer (Model HI96801, Hanna Instruments, Woonsocket, RI, USA) was used to determine TSS content (°Brix) of each fruit. As proposed by Ullah et al. (2018ab) and Maneepitak et al. (2019), irrigation water productivity (kg m^{-3}) was measured by dividing fruit yield (kg) by total irrigation water input (m^3) provided in each pot throughout the crop growth period.

Physio-biochemical parameters Leaf greenness was measured with a portable chlorophyll meter (SPAD-502 Plus, Minolta Corporation, Ltd., Osaka, Japan) from the fully-expanded fourth young leaf from the shoot tip of each plant at 4 weeks after imposing drought stress. To estimate LRWC, leaf was collected from the mid-section of each plant, followed by recording its fresh weight. Turgid weight

was recorded after 24 h of immersion of the leaf sample in deionized water at room temperature. Afterwards, the samples were dried in an oven at 80 °C until a constant dry weight was obtained, and LRWC was computed using the following equation (Jones and Turner 1978):

$$\text{LRWC (\%)} = \frac{(\text{Fresh weight} - \text{Dry weight})}{(\text{Turgid weight} - \text{Dry weight})} \times 100$$

Electrolyte leakage was determined by the method described by Camejo et al. (2005). The leaf sample was washed three times with distilled water and 1 cm^2 disk was placed in 20 mL deionized water containing test tube for incubation in a rotary shaker for 24 h (120 rpm). After determining electrical conductivity (EC_1), samples were autoclaved for 20 min at 120 °C, cooled, and electrical conductivity (EC_2) was measured again. The following equation was used to determine electrolyte leakage (%):

$$\text{Electrolyte leakage (\%)} = \frac{EC_1}{EC_2} \times 100$$

Membrane stability index was calculated using two samples of 1 cm^2 leaf disk in test tube with 20 mL deionized water (Hayat et al. 2008). The first electrical conductivity (EC_1) was measured after incubation for 30 min at 40 °C and the second electrical conductivity (EC_2) was noted after 10 min of incubation at 100 °C. Membrane stability index was calculated using the following equation:

$$\text{Membrane stability index (\%)} = (1 - \frac{EC_1}{EC_2}) \times 100$$

The proline concentration of leaf tissues was estimated using the method of Bates et al. (1973). At first, sulfosalicylic acid (3%) was mixed thoroughly with leaf sample (100 mg), followed by 15 min of centrifugation at 12,000 rpm. The reaction mixture was subsequently heated for 30 min at 100 °C using 2 mL of the supernatant and 2 mL of each of the ninhydrin solution and glacial acetic acid. The solution was derived using toluene and blended for 20 s in a vortex mixer. Finally, using toluene as a blank, the absorbance was measured spectrophotometrically at 520 nm. The equivalent proline concentration was estimated using a standard curve representing known proline concentrations and is expressed as μg g^{-1} fresh weight.

Between 09.30 and 11.30 am, leaf gas exchange parameters, such as P_n (μmol CO_2 m^{-2} s^{-1}), g_s (mmol H_2O m^{-2} s^{-1}), and E (mmol H_2O m^{-2} s^{-1}), of the third fully-expanded leaf from the shoot tip were measured using a portable photosynthesis system (LI-6400XT, Li-COR, Lincoln, NE, USA) following Cha-um et al. (2006). Measurements were initiated at approximately 370 ± 20 μmol mol^{-1} air CO_2 concentration in the assimilation chamber with an ambient temperature of 28 ± 1 °C. During the measurements, artificial illumination from a red-blue 6400-02B LED light source that could emit continuous light at 1,000 μmol m^{-2} s^{-1} photosynthetic photon flux density was used.

3.2 Statistical Analysis

The data were analyzed using the statistical software STAR 2.0.1 (Statistical Tool for Agricultural Research, version 2.0.1) (IRRI 2014). The significance of differences between mean values was determined by one-way (germination trial) or two-way analysis of variance (polyhouse experiment). Tukey's honest significant difference test was used to compare the treatment means at $P \leq 0.05$. Data on some of the morphological and physiological parameters (plant height, SPAD value, P_n, g_s, and E) were periodically collected and analyzed at 2-week intervals. However, the trend of significance remained similar in all cases. Therefore, data gathered at 4 weeks after transplanting are presented and discussed to avoid redundancy.

4 Results

4.1 Seed Germination Traits

Seed pretreatment with various materials had a significant effect on germination percentage, germination rate, germination energy, and mean germination time (Fig. 1). Germination percentage of primed seeds was much higher than that of the non-primed control seeds, except for SA priming where germination percentage was similar to the non-primed control seeds (Fig. 1a). Priming with KNO_3 had an overall better performance with the highest germination percentage (Fig. 1a), germination rate (Fig. 1b), germination energy (Fig. 1c), and lowest mean germination time (Fig. 1d). There was no difference in germination energy and mean germination time of the non-primed control and hydroprimed seeds. However, germination percentage and germination rate of hydroprimed seeds were significantly higher than the non-primed control seeds.

4.2 Morphological and Reproductive Parameters

Plant height, leaf number per plant, shoot dry matter, and root dry matter were highly significantly affected by the two-way interaction between seed priming and soil moisture regime, whereas days to flowering, days to fruit set, and days to fruit maturity were only affected by the main effect of seed priming and soil moisture

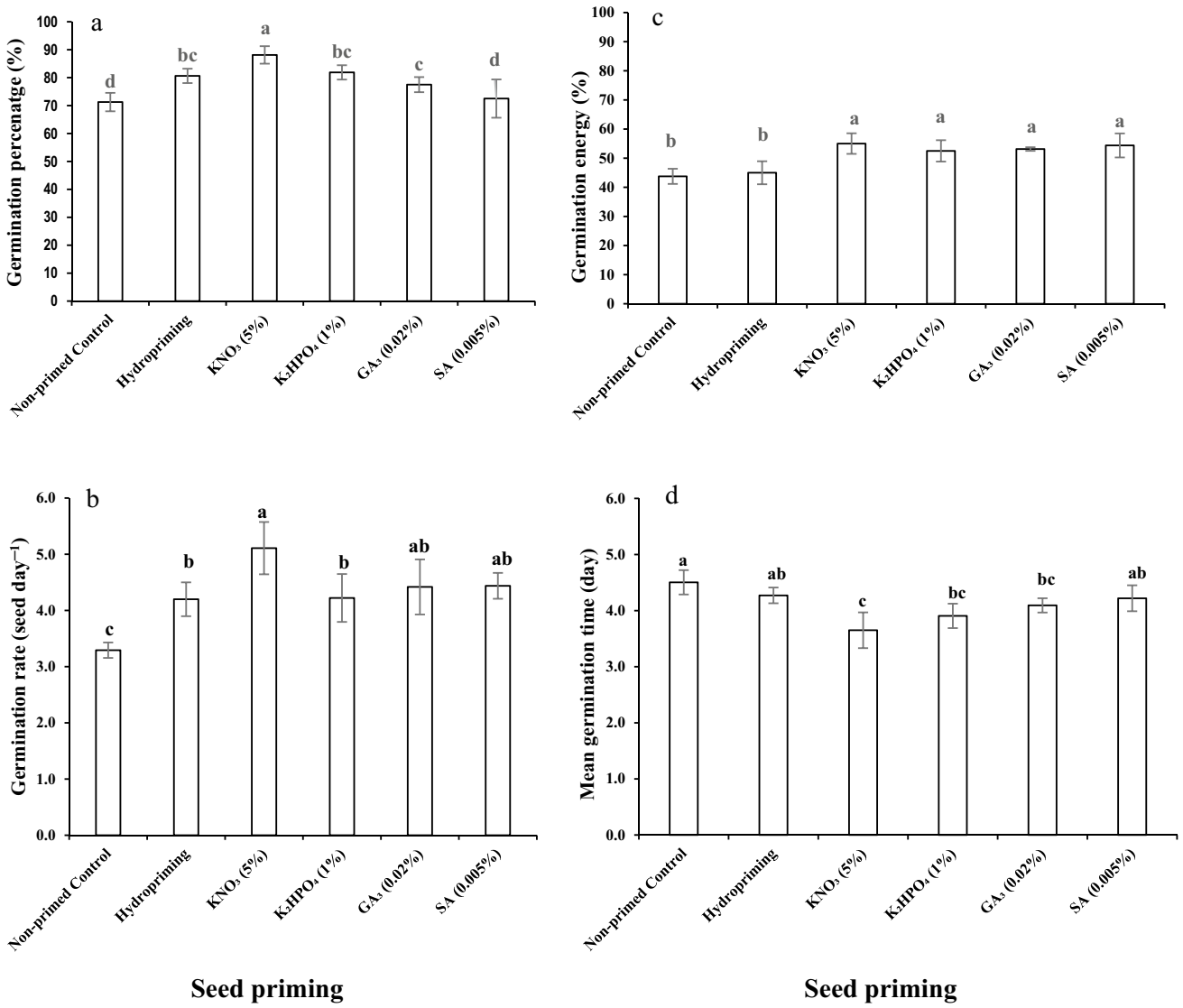

Fig. 1 Effect of seed priming on germination percentage (**a**), germination rate (**b**), germination energy (**c**), and mean germination time (**d**) of cucumber. KNO_3, potassium nitrate; K_2HPO_4, dipotassium phosphate; GA_3, gibberellic acid; SA, salicylic acid. Bars show means of four replications ± standard errors. Bars with same letters are not significantly different based on Tukey's honest significant difference test at $P \leq 0.05$

regime (Table 1). Seed priming with KNO_3 outperformed other treatments across soil moisture regimes, while other priming treatments were mostly ineffective and resulted in similar growth as the non-primed control plants, especially at the lowest soil moisture level of 40% FC (Table 2). An increase of 30–68%, 18–68%, 30–68%, and 17–60% was evident in plant height, leaf number per plant, shoot dry matter, and root dry matter, respectively, of plants raised from seeds primed with KNO_3 compared with the non-primed control plants across soil moisture regimes. Decreasing soil moisture level from 100 to 40% FC caused a 36–49%, 36–51%, 37–48%, and 53–69% decrease in plant height, leaf number per plant, shoot dry matter, and root dry matter, respectively, across seed priming doses.

Flowering, fruit set, and fruit maturity were delayed in the non-primed control plants, while seed priming caused early flowering in all plants regardless of priming materials (Table 2). However, there was largely no difference among the non-primed control plants and all priming treatments in their days to fruit set and days to fruit maturity, except for plants raised from seeds primed with KNO_3 where these durations were significantly shorter.

Table 1 Significance levels in two-way ANOVA of the effect of seed priming, soil moisture regime, and their interaction on morphological and reproductive parameters, fruit yield parameters, fruit quality, irrigation water productivity, and physio-biochemical parameters of cucumber

Parameter	Seed priming	Soil moisture regime	Seed priming × soil moisture regime
Morphological and reproductive parameters			
Plant height (cm)	**	**	**
Leaf number per plant	**	**	**
Shoot dry matter (g plant^{-1})	**	**	**
Root dry matter (g plant^{-1})	**	**	**
Days to flowering	**	**	ns
Days to fruit set	**	**	ns
Days to fruit maturity	**	**	ns
Fruit yield parameters, fruit quality, and irrigation water productivity			
Fruit number per plant	**	**	**
Fruit length (cm)	**	**	**
Fruit diameter (cm)	**	**	ns
Fruit weight (gm)	**	**	**
Fruit yield (g plant^{-1})	**	**	**
Total soluble solids (°Brix)	**	**	ns
Irrigation water productivity (kg m^{-3})	**	**	**
Physio-biochemical parameters			
Leaf greenness (SPAD value)	**	**	**
Leaf relative water content (%)	**	**	*
Electrolyte leakage (%)	**	**	**
Membrane stability index (%)	**	**	**
Net photosynthetic rate (µmol CO_2 m^{-2} s^{-1})	**	**	**
Stomatal conductance (mmol H_2O m^{-2} s^{-1})	**	**	**
Transpiration rate (mmol H_2O m^{-2} s^{-1})	**	**	**
Free proline concentration (µg g^{-1} fresh weight)	**	**	**

*, **, and ns represent significant ($P \leq 0.05$), highly significant ($P \leq 0.01$), and non-significant, respectively

4.3 Fruit Yield Parameters, Fruit Yield, Fruit Quality, and Irrigation Water Productivity

The interaction between seed priming and soil moisture regime had a highly significant effect on fruit number per plant, fruit length, and fruit weight, whereas fruit diameter was highly significantly affected by the main effect of seed priming and soil moisture regime (Table 1). Seed priming with GA_3, SA, and hydropriming largely remained ineffective in increasing fruit number per plant, especially at lower soil moisture regimes, while priming with KNO_3 had the highest fruit number per plant regardless of soil moisture regimes (60–100% higher than the non-primed control across soil moisture regimes) (Table 3). Decreasing soil moisture from 100 to 40% FC caused a 57–71% reduction in fruit number per plant across seed priming treatments with the least reduction for KNO_3 (57%) and the highest reduction (71%) for SA priming. Fruit length and fruit weight response largely remained similar for hydropriming, K_2HPO_4 priming, GA_3 priming, and SA priming regardless of soil moisture regimes (Table 3). The plants raised from seeds primed with KNO_3 had the highest fruit length and fruit weight, which were significantly higher than the non-primed control at all soil moisture regimes. Fruit length and fruit weight were increased by 9–20% and 50–104%, respectively, for KNO_3-primed plants compared with the non-primed control across soil moisture regimes. A significant reduction in fruit length (32–37%) and fruit weight (30–51%) was evident across seed priming doses at reduced soil moisture level of 40% FC compared with 100% FC. The main effect of seed priming and soil moisture regime indicated that fruit diameter of plants raised from KNO_3-primed seeds was significantly higher than all other priming treatments with a maximum increase of 14% than the non-primed control plants, while a progressive reduction in fruit diameter was observed with decreasing soil moisture regime (12% reduction at 40% FC compared with 100% FC) (Table 3).

The interaction between seed priming and soil moisture regime had a highly significant ($P < 0.01$) effect on fruit yield and irrigation water productivity, whereas TSS content was highly significantly affected by the main effect of seed priming and soil moisture regime (Table 1). Fruit yield response

Table 2 Effect of seed priming and soil moisture regime on morphological (plant height, leaf number per plant, shoot dry matter, and root dry matter) and reproductive parameters (days to flowering, days to fruit set, and days to fruit maturity) of cucumber

Factor		Plant height (cm)	Leaf number per plant	Shoot dry matter (g plant^{-1})	Root dry matter (g plant^{-1})	Days to flowering	Days to fruit set	Days to fruit maturity
Seed priming								
Non-primed control		133.9 ± 6.44c	31.8 ± 1.52d	12.8 ± 0.62c	1.1 ± 0.09 cd	28.8 ± 0.47a	12.0 ± 0.62a	9.1 ± 0.56a
Hydropriming		141.9 ± 7.37bc	33.6 ± 1.75c	13.6 ± 0.70bc	1.0 ± 0.10d	27.4 ± 0.40b	11.2 ± 0.43a	8.2 ± 0.52a-c
KNO_3		185.0 ± 9.50a	43.1 ± 2.13a	17.6 ± 0.91a	1.3 ± 0.09a	26.6 ± 0.44b	9.9 ± 0.38b	7.4 ± 0.43c
K_2HPO_4		148.5 ± 8.84b	35.3 ± 2.21bc	14.0 ± 0.83b	1.1 ± 0.10bc	26.6 ± 0.46b	11.4 ± 0.59a	7.8 ± 0.48bc
GA_3		147.3 ± 8.69b	35.1 ± 2.04bc	14.1 ± 0.83b	1.1 ± 0.11b	27.3 ± 0.38b	11.2 ± 0.55a	8.1 ± 0.50a-c
SA		147.7 ± 8.33b	35.5 ± 1.95b	14.0 ± 0.79b	1.0 ± 0.09d	27.3 ± 0.39b	12.0 ± 0.53a	8.8 ± 0.56ab
Soil moisture regime								
40% FC		101.6 ± 2.63d	24.0 ± 0.55d	9.7 ± 0.21d	0.6 ± 0.02d	29.1 ± 0.27a	13.8 ± 0.28a	10.7 ± 0.30a
60% FC		151.3 ± 5.27c	36.0 ± 1.22c	14.5 ± 0.51c	1.1 ± 0.03c	27.6 ± 0.32b	11.9 ± 0.29b	8.5 ± 0.29b
80% FC		169.7 ± 3.96b	40.0 ± 0.86b	16.0 ± 0.39b	1.3 ± 0.02b	26.8 ± 0.30b	10.4 ± 0.24c	7.3 ± 0.28c
100% FC		180.3 ± 3.77a	42.8 ± 0.78a	17.2 ± 0.35a	1.5 ± 0.02a	25.8 ± 0.20c	9.1 ± 0.23d	6.4 ± 0.19c
Seed priming × soil moisture regime								
Non-primed control	40% FC	103.0 ± 5.73i-k	24.5 ± 0.50hi	9.8 ± 0.35jk	0.5 ± 0.01 l	31.0 ± 0.41	15.3 ± 0.47	11.8 ± 0.77
	60% FC	119.0 ± 3.37ij	28.0 ± 0.91gh	11.4 ± 0.21ij	1.0 ± 0.08 h-j	29.0 ± 0.71	12.5 ± 0.75	9.4 ± 0.81
	80% FC	151.8 ± 3.82e-g	36.3 ± 0.63d-f	14.4 ± 0.41f-h	1.2 ± 0.03 fg	28.3 ± 0.85	10. ± 0.59	8.0 ± 0.77
	100% FC	161.8 ± 3.57d-g	38.5 ± 0.65c-f	15.5 ± 0.53d-h	1.4 ± 0.04b-d	27.0 ± 0.41	9.5 ± 0.62	7.1 ± 0.53
Hydropriming	40% FC	95.5 ± 3.80 k	22.5 ± 0.65i	9.1 ± 0.10 k	0.5 ± 0.05 l	29.3 ± 0.48	13.2 ± 0.45	10.7 ± 0.65
	60% FC	148.8 ± 3.57 fg	35.3 ± 1.11f	14.3 ± 0.17f-h	0.9 ± 0.04j-k	27.5 ± 0.65	11.8 ± 0.65	8.5 ± 0.74
	80% FC	155.8 ± 3.86d-g	36.8 ± 1.11d-f	14.9 ± 0.38e-h	1.2 ± 0.05f-i	26.5 ± 0.65	10.2 ± 0.50	7.3 ± 0.70
	100% FC	167.5 ± 5.33c-f	39.8 ± 0.85c-e	16.0 ± 0.43d-g	1.5 ± 0.01b-d	26.3 ± 0.48	9.7 ± 0.30	6.3 ± 0.41
KNO_3	40% FC	123.8 ± 4.77hi	29.0 ± 0.71 g	11.7 ± 0.32ij	0.8 ± 0.03 k	28.0 ± 0.71	11.8 ± 0.34	9.5 ± 0.59
	60% FC	200.5 ± 4.66ab	47.0 ± 0.91a	19.2 ± 0.42a-c	1.2 ± 0.03e-g	27.0 ± 1.22	10.4 ± 0.40	7.6 ± 0.57
	80% FC	205.0 ± 4.95ab	47.5 ± 0.65a	19.5 ± 0.55ab	1.4 ± 0.01c-e	26.0 ± 0.41	9.2 ± 0.47	6.5 ± 0.66
	100% FC	210.8 ± 7.19a	48.8 ± 0.85a	20.1 ± 0.39a	1.7 ± 0.02a	25.3 ± 0.48	8.4 ± 0.26	6.0 ± 0.49
K_2HPO_4	40% FC	95.5 ± 3.40 k	22.0 ± 0.82i	9.1 ± 0.13 k	0.5 ± 0.03 l	28.5 ± 0.65	14.2 ± 0.48	10.2 ± 0.74
	60% FC	148.3 ± 3.88 fg	35.5 ± 0.65ef	14.0 ± 0.44gh	1.0 ± 0.02ij	26.8 ± 0.75	12.2 ± 0.42	8.1 ± 0.63
	80% FC	162.8 ± 3.33d-g	38.5 ± 1.04c-f	15.2 ± 0.46e-h	1.3 ± 0.03d-g	26.3 ± 0.95	10.2 ± 0.50	6.8 ± 0.64
	100% FC	187.5 ± 3.88bc	45.0 ± 1.29ab	17.6 ± 0.64b-d	1.6 ± 0.03ab	25.0 ± 0.41	8.8 ± 0.80	6.2 ± 0.45
GA_3	40% FC	93.3 ± 3.42 k	22.5 ± 0.65i	8.9 ± 0.16 k	0.5 ± 0.02 l	29.0 ± 0.41	13.9 ± 0.54	10.5 ± 0.64
	60% FC	149 ± 4.02 fg	35.3 ± 1.25f	14.4 ± 0.35f-h	1.2 ± 0.03 g-i	27.5 ± 0.65	11.7 ± 0.73	8.4 ± 0.74
	80% FC	169.3 ± 4.91c-f	40.0 ± 1.29 cd	15.9 ± 0.62d-g	1.3 ± 0.01d-f	26.8 ± 0.63	103 ± 0.57	7.2 ± 0.70
	100% FC	177.8 ± 3.88 cd	42.5 ± 0.87bc	17.0 ± 0.42c-e	1.6 ± 0.02a-c	25.8 ± 0.25	9.1 ± 0.84	6.3 ± 0.42
SA	40% FC	98.5 ± 2.90jk	23.8 ± 0.48hi	9.5 ± 0.25jk	0.5 ± 0.02 l	29.0 ± 0.41	14.4 ± 0.43	11.6 ± 0.81
	60% FC	142.3 ± 3.45gh	34.8 ± 1.11f	13.4 ± 0.50hi	1.0 ± 0.02j	27.8 ± 0.48	12.6 ± 0.97	9.0 ± 0.83
	80% FC	173.5 ± 4.99c-e	41.3 ± 0.85bc	16.3 ± 0.67d-f	1.2 ± 0.02f-h	26.8 ± 0.63	11.7 ± 0.39	7.8 ± 0.75
	100% FC	176.5 ± 5.17 cd	42.3 ± 1.11bc	17.0 ± 0.55de	1.5 ± 0.05b-d	25.5 ± 0.29	9.5 ± 0.45	6.9 ± 0.52

KNO_3, potassium nitrate; K_2HPO_4, dipotassium phosphate; GA_3, gibberellic acid; SA, salicylic acid; FC, field capacity. Means followed by the same letters within a column are statistically similar based on Tukey's honest significant difference test at $P \leq 0.05$; data are means of four replications ± standard errors

Table 3 Effect of seed priming and soil moisture regime on fruit yield parameters (fruit number per plant, fruit length, fruit diameter, and fruit weight) of cucumber

Factor		Fruit number per plant	Fruit length (cm)	Fruit diameter (cm)	Fruit weight (g)
Seed priming					
Non-primed control		2.0 ± 0.18d	10.5 ± 0.46d	3.6 ± 0.08e	74.3 ± 2.86e
Hydropriming		2.2 ± 0.21c	11.1 ± 0.41c	3.7 ± 0.06de	81.7 ± 2.81d
KNO_3		3.5 ± 0.25a	11.7 ± 0.44a	4.1 ± 0.03a	144.8 ± 9.07a
K_2HPO_4		2.7 ± 0.25b	11.6 ± 0.47ab	3.9 ± 0.06bc	121.2 ± 6.97b
GA_3		2.3 ± 0.22c	11.3 ± 0.44c	3.8 ± 0.06 cd	110.3 ± 5.90c
SA		2.3 ± 0.22c	11.4 ± 0.45bc	3.9 ± 0.05b	112.1 ± 5.92c
Soil moisture regime					
40% FC		1.2 ± 0.08d	8.5 ± 0.11d	3.6 ± 0.05d	71.7 ± 1.92d
60% FC		2.4 ± 0.12c	11.4 ± 0.08c	3.8 ± 0.05c	111.0 ± 5.82c
80% FC		2.9 ± 0.11b	12.3 ± 0.08b	3.9 ± 0.04b	121.5 ± 6.08b
100% FC		3.5 ± 0.12a	12.9 ± 0.13a	4.1 ± 0.02a	125.5 ± 6.24a
Seed priming × soil moisture regime					
Non-primed control	40% FC	1.0 ± 0.00j	7.5 ± 0.13 k	3.4 ± 0.12 h	56.9 ± 1.04 m
	60% FC	1.8 ± 0.10i	10.9 ± 0.15i	3.5 ± 0.05f-h	73.6 ± 1.23kl
	80% FC	2.5 ± 0.09f-h	11.7 ± 0.11f-h	3.6 ± 0.10e-h	81.9 ± 0.74i-k
	100% FC	2.8 ± 0.09ef	11.9 ± 0.15e-h	4.1 ± 0.07a-c	84.7 ± 1.84 h-j
Hydropriming	40% FC	1.0 ± 0.00j	8.5 ± 0.09j	3.5 ± 0.03gh	65.1 ± 2.25 lm
	60% FC	2.1 ± 0.09hi	11.4 ± 0.16 g-i	3.7 ± 0.09d-h	80.2 ± 1.21i-k
	80% FC	2.8 ± 0.08ef	12.1 ± 0.12d-g	3.8 ± 0.03b-g	88.8 ± 0.41hi
	100% FC	3.2 ± 0.08de	12.5 ± 0.13b-e	4.0 ± 0.02a-c	92.7 ± 1.31 h
KNO_3	40% FC	2.0 ± 0.00hi	9.0 ± 0.14j	4.0 ± 0.04a-c	85.4 ± 1.23 h-j
	60% FC	3.4 ± 0.13 cd	11.6 ± 0.17 g-i	4.1 ± 0.05ab	153.8 ± 2.58b
	80% FC	4.0 ± 0.13b	12.7 ± 0.11b-d	4.2 ± 0.08a	167.4 ± 1.10a
	100% FC	4.6 ± 0.12a	13.6 ± 0.15a	4.2 ± 0.01a	172.7 ± 2.32a
K_2HPO_4	40% FC	1.3 ± 0.25j	8.7 ± 0.13j	3.7 ± 0.05d-h	75.6 ± 0.54jk
	60% FC	2.7 ± 0.05ef	11.9 ± 0.11e-h	3.8 ± 0.07b-f	129.1 ± 3.31de
	80% FC	3.2 ± 0.04de	12.4 ± 0.11b-e	3.9 ± 0.08a-e	137.7 ± 1.62 cd
	100% FC	3.8 ± 0.04bc	13.4 ± 0.21a	4.2 ± 0.05a	142.3 ± 2.45c
GA_3	40% FC	1.0 ± 0.00j	8.5 ± 0.12j	3.5 ± 0.06f-h	72.7 ± 1.15kl
	60% FC	2.2 ± 0.17 g-i	11.4 ± 0.08 g-i	3.6 ± 0.06d-h	113.2 ± 3.10 g
	80% FC	2.6 ± 0.11 fg	12.4 ± 0.04c-f	3.9 ± 0.05a-e	125.8 ± 2.80ef
	100% FC	3.3 ± 0.13d	12.9 ± 0.14a-c	4.1 ± 0.05a-c	129.5 ± 1.21de
SA	40% FC	1.0 ± 0.00j	8.6 ± 0.17j	3.7 ± 0.08c-g	74.3 ± 1.10kl
	60% FC	2.2 ± 0.07 g-i	11.2 ± 0.05hi	3.9 ± 0.05a-d	116.2 ± 4.26 fg
	80% FC	2.7 ± 0.07ef	12.5 ± 0.10b-e	3.9 ± 0.04a-e	127.2 ± 1.36e
	100% FC	3.4 ± 0.07 cd	13.1 ± 0.19ab	4.2 ± 0.03a	130.9 ± 1.87de

KNO_3, potassium nitrate; K_2HPO_4, dipotassium phosphate; GA_3, gibberellic acid; SA, salicylic acid; FC, field capacity. Means followed by the same letters within a column are statistically similar based on Tukey's honest significant difference test at $P \leq 0.05$; data are means of four replications ± standard errors

largely remained similar for hydropriming, K_2HPO_4 priming, GA_3 priming, and SA priming regardless of soil moisture regimes (Table 4). The plants raised from seeds primed with KNO_3 had the highest fruit yield and irrigation water productivity, which were significantly higher than the non-primed control at all soil moisture regimes. Fruit yield was increased by 214–284% for KNO_3-primed plants compared with the non-primed control across soil moisture regimes. A significant reduction in fruit yield (77–84%) was evident across seed priming doses at reduced soil moisture condition of 40% FC compared with 100% FC. Irrigation water productivity reflected a similar trend like fruit yield and was the highest for KNO_3-primed plants, while other priming treatments had largely similar irrigation water productivity with that of the non-primed control plants, especially at a lower soil moisture regime of 40% FC (Table 4). Seed priming with KNO_3

Table 4 Effect of seed priming and soil moisture regime on fruit yield, total soluble solids content, and irrigation water productivity of cucumber

Factor		Fruit yield (g plant^{-1})	Total soluble solids (%)	Irrigation water productivity (kg m^{-3})
Seed priming				
Non-primed control		167.3 ± 19.48d	3.2 ± 0.15b	5.67 ± 0.24e
Hydropriming		202.3 ± 23.89d	3.3 ± 0.14b	7.27 ± 0.42d
KNO_3		552.0 ± 63.36a	3.6 ± 0.13a	18.41 ± 0.91a
K_2HPO_4		366.3 ± 44.95b	3.6 ± 0.14a	12.51 ± 0.87b
GA_3		280.2 ± 37.45c	3.4 ± 0.16b	8.95 ± 0.59c
SA		288.5 ± 37.44c	3.3 ± 0.14b	9.35 ± 0.48c
Soil moisture regime				
40% FC		88.8 ± 8.55d	4.1 ± 0.05a	7.10 ± 0.65d
60% FC		296.5 ± 29.54c	3.6 ± 0.05b	12.63 ± 1.10a
80% FC		384.0 ± 33.02b	3.3 ± 0.06c	11.49 ± 0.98b
100% FC		468.5 ± 38.84a	2.7 ± 0.06d	10.22 ± 0.85c
Seed priming × soil moisture regime				
Non-primed control	40% FC	56.9 ± 1.78 m	3.9 ± 0.15	4.87 ± 0.40n
	60% FC	144.3 ± 7.10 k-m	3.5 ± 0.17	6.04 ± 0.33 l-n
	80% FC	217.6 ± 9.03i-k	3.2 ± 0.09	6.43 ± 0.64 k-n
	100% FC	250.3 ± 8.41 h-k	2.4 ± 0.09	5.36 ± 0.17 mn
Hydropriming	40% FC	65.1 ± 5.34 lm	3.9 ± 0.11	4.88 ± 0.67n
	60% FC	178.3 ± 5.96j-l	3.5 ± 0.11	8.86 ± 0.14 h-k
	80% FC	260.6 ± 10.05 g-j	3.2 ± 0.15	8.20 ± 0.20i-l
	100% FC	305.2 ± 11.30 g-i	2.6 ± 0.09	7.14 ± 0.26j-n
KNO_3	40% FC	170.3 ± 3.35j-m	4.2 ± 0.06	13.07 ± 0.71ef
	60% FC	554.3 ± 39.93 cd	3.8 ± 0.14	22.03 ± 0.69a
	80% FC	683.9 ± 2.87b	3.6 ± 0.18	20.46 ± 0.19ab
	100% FC	799.4 ± 46.06a	3.0 ± 0.10	18.08 ± 0.54bc
K_2HPO_4	40% FC	94.4 ± 18.77 lm	4.3 ± 0.06	7.85 ± 1.15i-m
	60% FC	366.7 ± 13.18e-g	3.8 ± 0.06	16.31 ± 0.70 cd
	80% FC	444.8 ± 17.76d-f	3.6 ± 0.14	14.14 ± 0.43de
	100% FC	559.4 ± 20.56c	2.9 ± 0.10	11.74 ± 0.24e-g
GA_3	40% FC	72.8 ± 5.37 lm	4.1 ± 0.09	5.46 ± 0.45 mn
	60% FC	268.4 ± 35.59 g-j	3.6 ± 0.11	11.49 ± 0.43 fg
	80% FC	336.8 ± 29.34f-h	3.2 ± 0.14	9.38 ± 0.41 g-j
	100% FC	443.0 ± 40.11d-f	2.5 ± 0.12	9.48 ± 0.28 g-j
SA	40% FC	73.1 ± 4.71 lm	4.0 ± 0.09	6.45 ± 0.49 k-n
	60% FC	266.8 ± 17.50 g-j	3.6 ± 0.09	11.07 ± 0.39f-h
	80% FC	360.3 ± 23.07e-h	3.2 ± 0.14	10.36 ± 0.19 g-i
	100% FC	453.8 ± 27.07c-e	2.6 ± 0.11	9.51 ± 0.25 g-j

KNO_3, potassium nitrate; K_2HPO_4, dipotassium phosphate; GA_3, gibberellic acid; SA, salicylic acid; FC, field capacity. Means followed by the same letters within a column are statistically similar based on Tukey's honest significant difference test at $P \leq 0.05$; data are means of four replications ± standard errors

caused more than 2- to-threefold increase in irrigation water productivity across soil moisture regimes compared with the non-primed control plants. Among four soil moisture regimes, the non-primed control plants had the highest irrigation water productivity at 80% FC (32% higher than irrigation water productivity at 40% FC), while all other priming treatments had the highest irrigation water productivity at 60% FC. Plants primed with KNO_3 and K_2HPO_4 had the highest TSS content (3.6%), which was 13% higher than that at the non-primed control (Table 4). Decreasing soil moisture caused a gradual increase in TSS content, and plants at 40% FC had 52% higher TSS content than that at 100% FC.

Table 5 Effect of seed priming and soil moisture regime on physio-biochemical parameters (leaf greenness, leaf relative water content, electrolyte leakage, membrane stability index, and free proline concentration) of cucumber

Factor		Leaf greenness (SPAD value)	Leaf relative water content (%)	Electrolyte leakage (%)	Membrane stability index (%)	Free proline concentration (μg g^{-1} fresh weight)
Seed priming						
Non-primed control		41.3 ± 1.18c	80.6 ± 1.08c	58.2 ± 2.00a	34.7 ± 1.84c	21.0 ± 4.49b
Hydropriming		43.2 ± 1.76b	82.8 ± 1.23b	48.9 ± 2.45b	35.6 ± 1.99c	17.5 ± 1.38bc
KNO_3		45.0 ± 1.90a	86.7 ± 0.63a	45.0 ± 1.66 cd	42.7 ± 2.24a	25.8 ± 1.95a
K_2HPO_4		41.3 ± 1.11c	83.5 ± 0.81b	48.4 ± 3.27bc	31.2 ± 1.83d	12.5 ± 0.75d
GA_3		43.8 ± 1.77ab	82.8 ± 1.04b	44.8 ± 3.30d	38.1 ± 2.42b	16.9 ± 0.91c
SA		42.8 ± 1.76bc	84.0 ± 0.90b	49.8 ± 2.10b	35.7 ± 1.94c	16.7 ± 0.74c
Soil moisture regime						
40% FC		50.1 ± 0.73a	78.5 ± 0.69d	61.9 ± 1.05a	24.5 ± 0.75d	26.6 ± 2.54a
60% FC		45.3 ± 0.61b	83.0 ± 0.52c	51.3 ± 1.37b	35.4 ± 0.51c	20.0 ± 1.16b
80% FC		42.0 ± 0.40c	84.7 ± 0.43b	44.8 ± 1.29c	41.1 ± 1.18b	15.4 ± 0.96c
100% FC		34.2 ± 0.37d	87.4 ± 0.49a	38.8 ± 1.68d	44.4 ± 0.97a	11.6 ± 1.17d
Seed priming × soil moisture regime						
Non-primed control	40% FC	47.5 ± 0.22 cd	74.5 ± 1.42 l	66.9 ± 4.07a	24.3 ± 0.91 k	48.5 ± 2.44a
	60% FC	41.5 ± 0.92e-h	80.5 ± 0.35 g-k	62.0 ± 1.87a-c	34.3 ± 0.40 g-j	21.8 ± 1.84b-e
	80% FC	41.2 ± 0.20f-h	82.8 ± 0.32c-i	52.4 ± 1.17d-f	37.5 ± 2.39d-i	9.7 ± 0.39 g-i
	100% FC	35.1 ± 1.19i	84.5 ± 1.35a-h	51.3 ± 1.18e-g	42.7 ± 0.68b-d	3.8 ± 0.12i
Hydropriming	40% FC	50.1 ± 0.55bc	76.5 ± 1.15 k-l	63.2 ± 0.86a-b	23.4 ± 0.86 k	25.4 ± 1.36bc
	60% FC	45.5 ± 1.21d-f	82.6 ± 0.72d-i	50.2 ± 1.80e-g	35.3 ± 0.91f-j	17.2 ± 1.46c-h
	80% FC	45.3 ± 0.54d-g	83.0 ± 1.04c-i	43.5 ± 1.08 g-i	41.3 ± 0.49c-e	14.2 ± 1.21d-h
	100% FC	32.1 ± 0.08i	89.1 ± 0.66a	38.6 ± 1.16ij	42.6 ± 0.73 cd	13.1 ± 0.65e-h
KNO_3	40% FC	54.9 ± 2.23a	83.5 ± 0.84b-i	55.0 ± 1.83b-e	31.2 ± 0.76j	31.7 ± 4.97b
	60% FC	46.6 ± 0.72 cd	87.0 ± 1.06a-d	44.3 ± 1.05f-i	38.2 ± 0.38d-h	29.5 ± 1.82b
	80% FC	43.3 ± 0.77d-h	87.2 ± 0.78a-d	40.7 ± 1.63 h-i	48.3 ± 0.59ab	22.9 ± 2.54b-d
	100% FC	35.3 ± 0.71i	89.1 ± 0.34a	40.1 ± 0.93 h-j	53.3 ± 0.88a	19.0 ± 3.33c-f
K_2HPO_4	40% FC	45.6 ± 0.74de	79.9 ± 0.18 h-k	60.2 ± 0.80a-d	20.4 ± 0.35 k	14.5 ± 1.14d-h
	60% FC	44.2 ± 0.63d-h	81.5 ± 0.51f-j	54.5 ± 1.88c-e	31.9 ± 0.59ij	13.9 ± 0.99d-h
	80% FC	40.6 ± 0.46 h	85.2 ± 0.85a-g	51.6 ± 1.17d-g	33.4 ± 1.86 h-j	13.2 ± 1.27e-h
	100% FC	34.9 ± 0.80i	87.4 ± 0.59a-c	27.5 ± 1.11 k	39.3 ± 0.36d-g	8.7 ± 0.73hi
GA_3	40% FC	50.5 ± 0.47bc	77.4 ± 1.24j-l	63.7 ± 1.04ab	23.9 ± 0.97 k	19.3 ± 1.17c-f
	60% FC	49.9 ± 0.40bc	82.0 ± 0.65e-j	47.9 ± 3.07e-h	36.3 ± 1.35e-j	19.2 ± 1.09c-f
	80% FC	40.6 ± 0.50 h	85.3 ± 1.00a-f	36.2 ± 0.52i-k	46.0 ± 1.40bc	16.7 ± 1.37c-h
	100% FC	34.3 ± 0.94i	86.4 ± 1.59a-e	31.4 ± 0.70jk	46.2 ± 1.12bc	12.4 ± 1.19f-i
SA	40% FC	52.4 ± 0.18ab	79.0 ± 0.30i-l	62.7 ± 0.95a-c	23.7 ± 1.12 k	19.9 ± 0.79c-f
	60% FC	44.3 ± 0.78d-h	84.4 ± 0.98a-h	48.7 ± 1.03e-h	36.3 ± 0.94e-j	17.9 ± 0 .48c-g
	80% FC	41.1 ± 0.37 g-h	84.7 ± 0.75a-h	44.3 ± 2.12f-i	40.2 ± 1.51d-f	16.1 ± 0.66d-h
	100% FC	33.5 ± 0.51i	88.0 ± 0.77ab	43.7 ± 1.70fi	42.5 ± 0.87 cd	12.9 ± 0.90e-i

KNO_3, potassium nitrate; K_2HPO_4, dipotassium phosphate; GA_3, gibberellic acid; SA, salicylic acid; FC, field capacity. Means followed by the same letters within a column are statistically similar based on Tukey's honest significant difference test at $P \leq 0.05$; data are means of four replications ± standard errors

4.4 Physio-Biochemical Parameters

The interaction between seed priming and soil moisture regime had a significant effect on SPAD value, LRWC, electrolyte leakage, membrane stability index, P_n, g_s, E, and free proline concentration (Table 1). The interaction between seed priming and soil moisture regime indicated that SPAD value was higher at lower soil moisture levels and showed a significant reduction with increasing soil moisture regime, especially at 100% FC across seed priming treatments (Table 5). There was generally no significant difference in SPAD values among different seed priming treatments, including the non-primed control at higher

soil moisture levels, except at 40% FC where KNO_3-primed plants had the highest SPAD value. There was no difference in LRWC among seed priming treatments, including the non-primed control at 80% and 100% FC, and the same was also largely true for other soil moisture regimes, except for KNO_3-primed plants where LRWC at 40% and 60% FC was 12% and 8% higher than the non-primed control (Table 5). Decreasing soil moisture from 100 to 40% FC caused a 6–14% reduction in LRWC. Electrolyte leakage was the highest for the non-primed control plants regardless of soil moisture regimes; however, seed priming was generally ineffective at 40% FC (Table 5). All seed priming treatments had largely similar electrolyte leakage, while it was the lowest for KNO_3-primed plants at most of the soil moisture regimes. Plants grown from seeds primed with KNO_3 had 18–29% lower electrolyte leakage than the non-primed control plants across soil moisture regimes. Electrolyte leakage of well-watered plants (100% FC) was 23–54% lower than the plants grown at severe soil moisture stress of 40% FC across seed priming treatments. Membrane stability index was the lowest for the non-primed control plants, which was not improved by seed priming at most of the soil moisture levels, except for KNO_3-primed plants where it was 28%, 29%, and 25% higher than the non-primed control plants at 40%, 80%, and 100% FC, respectively (Table 5). The effect of decreasing soil moisture was evident in all plants where membrane stability index was reduced by 41–48% across seed priming treatments.

The non-primed control plants accumulated the highest free proline at 40% FC, which was significantly reduced by all seed priming treatments at the same soil moisture level (Table 5). However, free proline concentration was largely significantly higher for KNO_3-primed plants at other soil moisture levels compared with the non-primed control plants, with a maximum fivefold increase at 100% FC. Decreasing soil moisture caused more free proline accumulation in all plants regardless of seed priming treatments; however, this increase was the highest (about 12-fold) for the non-primed control plants at 40% FC compared with 100% FC.

Net photosynthetic rate, g_s, and E largely remained similar among priming treatments, including the non-primed control, especially at reduced soil moisture levels of 40%, 60%, and 80% FC (Table 6). At 100% FC, KNO_3-primed plants had 34%, 73%, and 39% higher P_n, g_s, and E, respectively, compared with the non-primed control plants. Net photosynthetic rate, g_s, and E were reduced by 33–46%, 45–68%, and 42–58% at reduced soil moisture level of 40% FC compared with 100% FC across seed priming doses.

5 Discussion

Drought is among the most devastating abiotic stresses as it has a direct negative impact on plant metabolism, development, and crop yield (Abdel-Ghany et al. 2020; Alam et al. 2021a). The frequency/severity of drought is exacerbated by rapid environmental changes limiting freshwater availability for major agricultural production systems around the world, especially in rainfed ecosystems (Bradford et al. 2017). Drought impacts are visible on seed germination, vegetative and reproductive growth, and maturation stages of a crop at different scales depending on the severity and the length of drought exposure (Anjum et al. 2017). Seed germination is among the major determinants of plant health and productivity and is a sensitive stage to water-deficit stress. Seed priming enhances embryonic growth and development by increasing the activity of various enzymes, such as amylase, protease, and lipase, that breakdown macromolecules resulting in an increase in total soluble sugar levels (Acharya et al. 2020; Farooq et al. 2021). This process helps seed germination under both stressful and normal environmental conditions. Different inorganic salts, plant growth regulators, organic chemicals, bioinoculants, macro or micronutrients, and plant-based natural extracts are used as seed priming materials to regulate plant water uptake (Farooq et al. 2019). Seed priming promotes seedling germination potential by enhancing its physiological and biochemical capacities, as well as preventing aging effects by maintaining a balance of malondialdehyde and ROS (Basra et al. 2003). Similar beneficial effects of seed priming were visible in various germination traits, such as germination percentage, germination rate, germination energy, and mean germination time (Fig. 1), compared with the non-primed control seeds, while KNO_3-primed seeds outperformed other priming materials in terms of germination percentage and germination rate. Seed priming with KNO_3 has been found effective in the synthesis of molecules that release nitric oxide (NO), which is highly beneficial in accelerating germination process under stressful conditions (Parankusam et al. 2017). The production of NO stimulates the availability of nitrates and inorganic nitrites in germinating seeds as a result of nitrite and nitrate decomposition (Nawaz et al. 2017). Nitrate-containing compounds have been reported to be more effective as priming materials than other salts (Nerson and Gover 1986). Seed-priming with salts like KNO_3 has been found to improve germination and growth of various vegetable crops under stressful conditions (Sowmya et al. 2013). These compounds affect membrane permeability, mitigating or correcting environmental stress damage. As water stress involves a change in osmotic potential and tension on the cellular membrane, it is likely that NO-releasing compounds can help with germination under abiotic stress (Shams et al. 2018; Ciacka et al. 2020). Nitric oxide is an important signaling molecule found in higher plants, and it is associated with the activation of growth and development of plants, pathogen protection, and abiotic stress responses (Parankusam et al. 2017).

Table 6 Effect of seed priming and soil moisture regime on leaf gas exchange parameters (net photosynthetic rate, stomatal conductance, and transpiration rate) of cucumber

Factor		Net photosynthetic rate (μmol CO_2 m^{-2} s^{-1})	Stomatal conductance (mmol H_2O m^{-2} s^{-1})	Transpiration rate (mmol H_2O m^{-2} s^{-1})
Seed priming				
Non-primed control		16.0 ± 0.81c	0.17 ± 0.01c	2.6 ± 0.15bc
Hydropriming		17.8 ± 0.89b	0.21 ± 0.03ab	2.9 ± 0.26ab
KNO_3		19.2 ± 1.07a	0.24 ± 0.02a	3.0 ± 0.22a
K_2HPO_4		18.2 ± 0.88b	0.20 ± 0.02bc	2.7 ± 0.20a-c
GA_3		18.4 ± 0.72ab	0.18 ± 0.02c	2.6 ± 0.20bc
SA		18.3 ± 0.86ab	0.18 ± 0.02c	2.5 ± 0.19c
Soil moisture regime				
40% FC		13.1 ± 0.26d	0.11 ± 0.01d	1.6 ± 0.05d
60% FC		17.9 ± 0.21c	0.18 ± 0.01c	2.6 ± 0.07c
80% FC		18.9 ± 0.26b	0.22 ± 0.01b	3.0 ± 0.08b
100% FC		22.0 ± 0.45a	0.28 ± 0.01a	3.5 ± 0.12a
Seed priming × soil moisture regime				
Non-primed control	40% FC	10.8 ± 0.40 h	0.12 ± 0.01f-i	1.8 ± 0.07f-i
	60% FC	16.7 ± 0.37f	0.18 ± 0.01e-h	2.6 ± 0.19d-f
	80% FC	17.7 ± 0.23ef	0.19 ± 0.01d-f	2.8 ± 0.22c-e
	100% FC	18.8 ± 0.35d-f	0.22 ± 0.01c-e	3.1 ± 0.19b-e
Hydropriming	40% FC	13.4 ± 0.38 g	0.11 ± 0.01 g-i	1.6 ± 0.09hi
	60% FC	17.5 ± 0.39ef	0.19 ± 0.01d-g	2.6 ± 0.14d-f
	80% FC	17.6 ± 0.26ef	0.21 ± 0.01c-e	2.9 ± 0.18c-e
	100% FC	22.9 ± 0.51ab	0.33 ± 0.02ab	3.8 ± 0.19ab
KNO_3	40% FC	13.6 ± 0.27 g	0.12 ± 0.01f-i	1.8 ± 0.06 g-i
	60% FC	18.4 ± 0.19ef	0.19 ± 0.02d-g	2.7 ± 0.11de
	80% FC	19.6 ± 0.42de	0.28 ± 0.02bc	3.6 ± 0.15a-c
	100% FC	25.1 ± 0.28a	0.38 ± 0.01a	4.3 ± 0.16a
K_2HPO_4	40% FC	13.4 ± 0.25 g	0.11 ± 0.01hi	1.5 ± 0.06i
	60% FC	17.5 ± 0.21ef	0.21 ± 0.02c-e	2.8 ± 0.20c-e
	80% FC	19.3 ± 0.94de	0.20 ± 0.03c-e	2.9 ± 0.10c-e
	100% FC	22.5 ± 0.57b	0.26 ± 0.01b-d	3.6 ± 0.21a-d
GA_3	40% FC	14.0 ± 0.44 g	0.09 ± 0.01i	1.4 ± 0.11i
	60% FC	19.3 ± 0.40de	0.17 ± 0.01e-i	2.6 ± 0.16e-g
	80% FC	19.7 ± 0.32c-e	0.22 ± 0.01c-e	3.1 ± 0.16b-e
	100% FC	20.8 ± 0.82b-d	0.24 ± 0.02c-e	3.2 ± 0.12b-e
SA	40% FC	13.2 ± 0.57gh	0.10 ± 0.01hi	1.5 ± 0.16i
	60% FC	18.3 ± 0.37ef	0.17 ± 0.02e-h	2.5 ± 0.14e-h
	80% FC	19.7 ± 0.33c-e	0.21 ± 0.02c-e	3.0 ± 0.13c-e
	100% FC	22.0 ± 0.54bc	0.24 ± 0.02c-e	3.2 ± 0.28b-e

KNO_3, potassium nitrate; K_2HPO_4, dipotassium phosphate; GA_3, gibberellic acid; SA, salicylic acid; FC, field capacity. Means followed by the same letters within a column are statistically similar based on Tukey's honest significant difference test at $P \leq 0.05$; data are means of four replications ± standard errors

In comparison to seedlings raised from non-primed and hydroprimed seeds, KNO_3-primed seedlings of cucumber performed better in terms of morphological traits, fruit yield, fruit quality, irrigation water productivity, and physio-biochemical parameters under water-deficit stress. Plants were taller with optimum soil moisture regime and primed seeds over the non-primed control. Seedlings raised from primed seeds grow at a faster rate, creating optimum competition among plants for nutrients, light, water, and space, resulting in taller plants. Drought stress first affects the root system, negatively affecting its morphology to respond to abiotic stress (Ming et al. 2012). A similar trend was also observed in the present study, where severe and moderate water-deficit stress (40% and 60% FC) significantly reduced root dry matter and shoot dry matter. Seed priming enhanced overall shoot and root biomass of cucumber even under moderate

and severe drought stress conditions. These findings are in accordance with other researchers who have mentioned that seed priming can enhance root biomass to a degree, which is beneficial to improving the root's ability to uptake water and nutrients from the soil (Miranda-Apodaca et al. 2018; Tausz-Posch et al. 2020). Anwar et al. (2020) observed that seed priming improved cucumber seedling growth, height, hypocotyl diameter, shoot fresh weight, and shoot dry weight compared with the untreated plants.

The results of the present study revealed that days to flowering, fruit set, and fruit maturity were significantly shorter for plants grown under well-watered condition of 100% FC with a gradual increase with decreasing soil moisture availability. These results are in agreement with Arshad (2017) who found that five-time drip irrigation shortened the time it took for greenhouse-grown cucumber to set flowers and fruits. Drought-induced delay in days to flowering, fruit set, and fruit maturity might be due to pollen sterility and fertility loss. On the other hand, seed priming with KNO_3 caused a significant reduction in the number of days to flowering, days to fruit set, and days to fruit maturity compared with the non-primed control plants. Seed priming helps in breaking seed dormancy, production of growth hormones, and faster growth leading toward early flowering and fruit set.

The number of fruits per plant is a major determinant of the final crop yield. A significant reduction in all yield contributing traits and fruit yield of cucumber was evident with decreasing soil moisture level, while seed priming with all chemicals was effective in enhancing yield attributes and fruit yield. However, seed priming with KNO_3 outperformed other priming treatments for fruit yield, especially at moderate to sufficient soil moisture availability. The findings are consistent with Ullah et al. (2002) who observed that priming increased yield characteristics, such as the number of primary branches per plant and the number of pods per plant of peela raya (*Brassica carinata* L.). Improved emergence and seedling growth are plausible explanations for such an increase in fruits number (Alam et al. 2021b, 2022). Well-watered condition of 100% FC in combination with KNO_3 seed priming resulted in the highest fruit yield of cucumber. Seed priming with KNO_3 also caused a substantial increase in irrigation water productivity across soil moisture regimes compared with the non-primed control plants. However, TSS content in fruits was markedly elevated by water-deficit stress, possibly due to the reduction in fruit size caused by drought stress, which has been linked to a decrease in fruit water content rather than a decrease in assimilates incorporated into the fruit (Chakma et al. 2021). Other researchers have also found similar results, indicating that elevated TSS content helps plants in sustaining osmotic pressure during stress conditions (Verma and Dubey 2001; Gupta et al. 2010).

Relative water content measures the amount of water in a cell and is linked to drought tolerance. The most reliable and effective method to measure plant water status under stress is to estimate LRWC of a plant (Zhang et al. 2021). Leaf relative water content is a better measure of the degree of cell and tissue hydration, which is vital for optimum metabolic activity and is a key drought indicator than absolute water content (Tomar and Kumar 2004; Silva et al. 2007). Extreme stress has a significant negative impact on LRWC when compared with the control group (Molnár et al. 2004). In the present study, LRWC improved with increasing irrigation amount. Stressed plants had a lower LRWC than plants grown under well-watered conditions. There is strong evidence that water stress decreases LRWC by dehydrating tissues in cucumber under drought stress (Zhang et al. 2013). The process of water and nutrient uptake by plant roots is adversely affected by membrane degradation under drought stress, which impacts the water content in plant. Plants grown from seeds primed with KNO_3 had higher LRWC than the non-primed control, especially at lower soil moisture regimes (40% and 60% FC).

Cell membrane stability and electrolyte leakage are inversely related. Drought stress increases the generation of ROS, which causes oxidative stress, especially in photosynthetic organelles. This causes lipid membranes to increase their permeability resulting in increased ion leakage. It was also evident in the present study that plants subjected to lower soil water availability had significantly lower cell membrane stability and higher electrolyte leakage compared with well-watered plants. The decrease in membrane stability index value with the increase in drought severity leads to the overproduction of ROS, which disrupts the cell membrane by altering its phospholipid and fatty acid compositions (Sun et al. 2020). The ability of a plant to maintain membrane stability and integrity would explain its tolerance against drought (Ahmadizadeh et al. 2011). A decrease in cell membrane stability under drought stress reflects the extent of lipid peroxidation caused by ROS (Sanchez-Rodrigue et al. 2010). Membrane stability index significantly increased and electrolyte leakage decreased in KNO_3-primed plants at all soil moisture levels, except for 60% FC, compared with the non-primed control plants. Seed priming promotes the production of antioxidant enzymes, reduces the accumulation of ROS in plants, and protects cell membrane integrity. Seed priming, especially with KNO_3, functions as a key mediator that modulates numerous metabolic pathways, including stomatal opening, increasing abscisic acid (drought stress hormone) catabolism, and improving antioxidant activity (Vidal et al. 2018; Gloser et al. 2020).

Accumulation of free proline was clearly enhanced in the leaves of cucumber seedlings exposed to moderate and severe drought conditions. Plants accumulate soluble sugars and proline under drought stress, which serve as osmolytes. These

compatible solutes assist in osmotic adjustments and membrane protein stabilization, thereby enhancing plant tolerance against drought stress. The concentrations of free proline in the priming treatments were considerably greater than in the non-primed treatment under moderate drought stress, indicating that priming helps mitigate the negative effects of drought stress. Plants have evolved many acclimation mechanisms to cope with drought stress. One of such mechanisms is to lower cell osmotic potential by increasing the number of solutes (proline, soluble sugar) that maintain cell turgor. Increased concentrations of these osmolytes in plants may be engaged in a variety of functions, including ROS detoxification, membrane integrity, activity stability of numerous enzymes, and osmotic adjustments, which in turn confer greater plant tolerance against drought stress (Blum 2017).

Leaf gas exchange parameter (P_n, g_s, and E) values were significantly higher in 100% FC compared with 40%, 60%, and 80% FC, most probably due to a drought-induced stomatal closure. Plants close their stomata to limit water loss to the atmosphere when soil moisture level falls below a certain limit, allowing them to maintain their water status under water-deficit stress (Liu et al. 2003). Drought stress-mediated drop in P_n has been reported to damage the photosystems, as well as inhibit Rubisco and other enzyme activities (Camejo et al. 2005). Seed priming markedly improved P_n, g_s, and E in cucumber seedlings compared with the non-primed control. Seed priming with KNO_3 has been reported to increase N and Mg accumulation in cucumber leaves, which are critical molecules in chlorophyll biosynthesis; therefore, it is possible that seed priming has improved cucumber seedling growth by increasing chlorophyll accumulation and photosynthetic capacity (Anwar et al. 2020). Ji et al. (2022) observed that seed priming increased photosynthetic performance and photochemical efficiency of photosystem II in cucumber plants, which could be the potential cause of better P_n, g_s, and E responses observed in the present study. Seed priming-induced improvement in photosynthetic performance enhances the tolerance potential of plants under stressful environments, resulting in higher yield and productivity (Tankari et al. 2021).

6 Conclusion

Drought stress had a substantial adverse impact on germination, seedling development, and physiological characteristics of cucumber. A drastic reduction in morphological traits, fruit yield, irrigation water productivity, and physiological attributes of cucumber were observed at severe water-deficit stress of 40% field capacity, and the same was largely true for 60% field capacity. Plant morphological parameters, flowering, fruit yield characteristics, and physio-biochemical indicators were used to demonstrate the favorable effects of seed priming on drought stress tolerance in cucumber plants. By enhancing germination-related parameters, seed priming aided in the sustainable production of cucumbers under drought stress. Plants grown from seeds primed with potassium nitrate exhibited more promising results (notably for chlorophyll formation and photosynthetic capacity, biomass accumulation, fruit yield, membrane stability index, and accumulation of free proline) than other priming treatments at moderate drought stress. Under severe (40% field capacity) and moderate (60% field capacity) drought stress conditions, potassium nitrate-primed plants outperformed non-primed and hydroprimed plants in all studied parameters. However, the effect was more pronounced under well-watered condition of 100% field capacity. The same priming material (potassium nitrate) was also generally more effective than the other evaluated priming materials. This eco-innovation improves cucumber plants' natural drought stress tolerance, resulting in higher crop yield and irrigation water productivity. Seed priming technique provides environmental and ethical safety, making it a potential and long-term strategy for ensuring food security under declining irrigation water availability.

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Data Availability The datasets used and/or analyzed during the current study are available from the corresponding author upon reasonable request.

Declarations

Conflict of Interest The authors declare no competing interests.

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