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Hydrogen Peroxide Supplementation in Irrigation Water Alleviates Drought Stress and Boosts Growth and Productivity of Potato Plants

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Citation: Abd Elhady, S.A.; El-Gawad, H.G.A.; Ibrahim, M.F.M.; Mukherjee, S.; Elkelish, A.; Azab, E.; Gobouri, A.A.; Farag, R.; Ibrahim, H.A.; El-Azm, N.A. Hydrogen Peroxide Supplementation in Irrigation Water Alleviates Drought Stress and Boosts Growth and Productivity of Potato Plants. *Sustainability* **2021**, *13*, 899. <https://doi.org/10.3390/su13020899>

Received: 1 December 2020

Accepted: 13 January 2021

Published: 17 January 2021

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Abstract: The present investigations aim to decipher the beneficial role of hydrogen peroxide-supplemented irrigation in imparting drought tolerance and promotion plant growth and yield of potato plants grown under two different irrigation regimes. Hydrogen peroxide injection (oxygenation) was applied at 0, 300, and 600 ppm through subsurface irrigation regimes on potato performance grown in heavy clay soil. The results indicated that oxygenation of irrigation water boosted the plant's vegetative growth and productivity, especially at 600 ppm hydrogen peroxide coupled with deficit irrigation. Root respiration, leaf biomass, chlorophyll content, and leaf osmotic status was observed to be improved in the presence of oxygenated irrigation. A similar trend was recorded on macro-elements (nitrogen, phosphorus, potassium and calcium content), proline, and soluble carbohydrates content of leaf along with catalase enzyme activity. Individual tuber weight, tuber number and tuber yield per plant and hectare recorded higher values as responding to oxygenated irrigation (300 and 600 ppm) of water within the optimum irrigation level. While the highest value of water use efficiency (WUE) was obtained by pairing deficit irrigation with 600 ppm oxygenated water. Thus, the present work provides new insights into the importance of oxygenated irrigation in obtaining optimum yield and field performance in potato plants subjected to deficit irrigation in clayey-loamy soils.

Keywords: potato (*Solanum tuberosum* L.); deficit irrigation; hydrogen peroxide; vegetative growth; tuber yield

1. Introduction

Potato (*Solanum tuberosum* L.) is a starch-yielding staple food crop that possesses immense economic and nutritive value. Among the various starch-yielding crops, it is ranked fourth after rice, wheat, and maize and has a substantial and increasing role for saving food worldwide [1]. It is grown in more than 100 countries worldwide [2] where

it can thrive and produce tubers in different environments and a wide range of soil [3]. Potato is a sensitive crop to drought stress, even if cultivars perform differently under the drought condition [4]. Moreover, potato plant roots are shallow and do not spread far outside the plowed surface layer of the soil [5]. The shallow-rooted crops are prone to a significant yield loss when exposed to drought stress [6]. The root volume and architecture is known to directly affect the strength of plant growth, productivity, and tolerance to different stresses, especially associated with the soil, such as soil compaction, drought, and salt stress [7].

Clay-loamy soils often suffer from poor oxygen levels in cultivation lands. Anoxic condition in the rhizosphere region of cultivable lands with shallow depth irrigation results in reduced root growth, poor field performance and reduced yield of plants. Thus, in view to assist cultivation in clayey-loamy soils with optimum water use, hydrogen peroxide (H_2O_2) application appears to be efficient in imparting oxygenated environments. Furthermore, exogenous H_2O_2 could enhance the growth, yield, osmoregulation, and antioxidative defense mechanism under deficit irrigation [8]. Fewer reports are available to substantiate the beneficial role of H_2O_2 -treated irrigation in potato cultivation under drought stress.

The plant root derives oxygen from the gaseous phase of the soil and the dissolved oxygen in the irrigation water. Since the proportion of the gaseous phase in soils is significantly reduced, the dissolved oxygen in irrigation water appears to be the main source of oxygen for plant root respiration [9]. Oxygenated irrigation, therefore, appears to be crucial for optimum growth and yield of the plants. One of the practices adopted by researchers to increase the dissolved oxygen concentration in the irrigation water is using hydrogen peroxide-mediated oxygenation [10]. In this context, H_2O_2 has been used as a plant growth promoter. It serves as a signaling molecule in some essential physiological processes such as photosynthesis, respiration, transmission, and transpiration where it is considered a regulator of the action of some genes in cells [11,12]. Thus, it has a regulatory effect on plant growth, development and yield. Most of the potato produced in Egypt grown in clay soils that suffer from compaction and lack of oxygen diffusion. Therefore it was substantial to investigate other soil practices that would reduce the deleterious impact of the heavy soils and improve the potato plant roots respiration thus leading to improved yield. Water stress management coupled with oxygenated irrigation appears to be of primary focus in optimizing crop yield and sustainability. Potato plants are sensitive to water deficiency throughout the growing season and, therefore, require frequent irrigation (60–80% of the available water capacity) [13–15]. To obtain high tuber yield and quality, a highly efficient irrigation system with ample oxygenation can significantly assist in reducing the risk of drought-induced yield loss in potato plants [16,17].

Various investigations reveal the beneficial role of hydrogen peroxide in regulating plant growth, metabolism and imparting tolerance to abiotic stress [11,12]. Although H_2O_2 is toxic at higher concentrations, its optimum endogenous concentration or in exogenous application might appear beneficial towards plant growth and signaling during abiotic stress. Hydrogen peroxide is a potent signaling molecule which modulates the function of various metabolic enzymes, promotes redox homeostasis, imparts osmotic tolerance and modulates ion exchange [10–12].

The present work aims to provide evidences for the beneficial role of hydrogen peroxide supplemented irrigation in alleviation of drought stress and improvement of growth and yield attributes in potato plants grown over two different irrigation regimes in clay soil.

2. Materials and Methods

2.1. Experimental Site

The experiment was conducted during two consecutive growing seasons of 2018 and 2019 in open field conditions at the experimental farm of the horticulture department which belonged to the experimental station of Faculty of Agriculture, Ain Shams University,

Shubra El-Kheima, Qaliubiya Governorate, Egypt (latitude $30^{\circ} \times 12' \text{ N}$, longitude $31^{\circ} 24' \text{ E}$, and means height 26 m above sea level). Soil pH and EC and some physical properties were shown in Table 1. Irrigational water was supplied from the Nile River (source located in the experimental area), with pH 7.2 and average electrical conductivity 0.63 dS m^{-1} . The seed tubers were planted on 5 February 2018, and on 7 February 2019, in the two planting seasons, respectively.

Table 1. Some physical properties, pH and EC of the experimental site soil.

Soil Depth	Texture	Soil Particle Distribution %			F.C.%	P.W.P.%	B.d.	Soil pH	Soil EC
cm		Sand	Silt	Clay	θ at −33 kPa	θ at −1500 kPa	g cm^{-3}		
0–30	Clay-loamy	24	36	40	−31.05	−1481	1.32	6.84	2.64
30–60	Clay-loamy	27	32	41	−32.71	−1768	1.34	6.82	2.67

F.C. = field capacity, P.W.P.= permanent wilting point, were determined as percentage in weight, B.d. = Bulk density and CL. = clay-loamy.

2.2. Experimental Treatments and Design

Spunta cultivar of potato (*Solanum tuberosum* L.) was used and its seed tubers were imported from the Netherlands by Daltex Corporation Company (. Potato seed tubers were planted on rows with 80 cm width and 20 cm between each other. The subsurface irrigation system was established for the experimental area before planting the potato seed tubers where each row has a buried one 16 mm drip line that has in-drippers every 25 cm. The dripping rate of the drippers was about 4 L per hour under the pressure of 1.5 bars. The chemical analyses of the water prove no salinity, carbonate or sulfate problem (Table 2).

Table 2. Some of the Nile water properties in the experiment location.

pH	TDS	HCO_3^-	CO_3^{2-}	Cl^-	SO_4^{2-}	Na^+
	mg/L			Meq/L		
7.2	403	0.5	0	2.5	1.28	1.7

The experiment had 6 treatments are a combination of 2 irrigation levels (deficit and optimum irrigation) and 3 hydrogen peroxide (H_2O_2) injection rates (0, 300, 600 ppm) with irrigation water. Irrigation was performed depending on soil water tension which was measured by a digital tensiometer that was used for monitoring the irrigation. The irrigation was onset at soil water tension 30 kPa then ended at 15 and 19 kPa for full and deficit irrigation, respectively. Irrigation onset at soil water tension 30 kPa and stopped at 15 kPa is the proper criterion for potato production in this experimental soil type and the drip irrigation system [18]. The H_2O_2 was injected at zero, 300 and 600 ppm with irrigation water. The program of irrigation and the H_2O_2 injection was started after the seed tubers sprouting complete, after 21 days from planting, and continued till maturation (100 days). The H_2O_2 was injected with every irrigation times at the end of the irrigation period. The H_2O_2 injection represented about 10% of the total irrigation period and quantity for both irrigation treatments. The amount of irrigation water was calculated via a water flow meter was installed at the entrance of the irrigated water supply. The H_2O_2 solution amount was calculated for each experimental plot as 10% of the consumed irrigation water quantity for the plot. The H_2O_2 solution amount was prepared in a polyethylene tank for each plot separately, then immediately injected using a submersible pump. The total quantity of the H_2O_2 solution applied per plot over each growing season was approximately 773 and 1104 L for the deficit and optimum irrigation treatments, respectively. The accumulated amount of irrigation water for each experimental plot over the growing season was 7730 and L when applied the deficit and optimum irrigation, respectively. The other agronomic

practices were carried out according to the potato production recommendations of the agricultural ministry in Egypt.

The experiment was designed as a simple trial and involved 6 treatments as shown in the following table. The experimental plot area was 24 m² and contains 3 rows 10 m long and 80 cm width. The plots were bordered by one untreated row. The treatments (Table 3) were distributed in a completely randomized block design with three replicates.

Table 3. The experimental treatments are a combination of irrigation level and hydrogen peroxide injection rate.

Irrigation Level	Hydrogen Peroxide Injection Rate		
	Zero (T1)	300 ppm (T2)	600 ppm (T3)
Deficit irrigation	Zero (T1)	300 ppm (T2)	600 ppm (T3)
Optimum irrigation	Zero (T4)	300 ppm (T5)	600 ppm (T6)

2.3. Data Recorded

2.3.1. Biomass

After 65 days of seed tuber planting and at the tuber initiation stage, four plants were chosen at random from each experimental plot, carefully be uprooted, and immediately transferred to the lab then subjected to measure the following parameters. Measuring the number of the stem per each plant and the average length of the main stem. The plant shoot and root were separated from each other. Each of both was dried at 70 °C till constant the weight then recording shoot and root dry weight as well as calculating root to shoot ratio based the dry weight.

2.3.2. Root Respiration ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)

The root respiration rate was measured by the alkali absorption method described by Saprnov and Kuzyakov [19]. 2 g of soil-free fresh roots were kept in a sealed glass vessel. The carbon dioxide gas resulting from the root respiration was received in a measuring flask containing a certain volume of NaOH solution 0.01 N for 12 h between 9 a.m. to 9 p.m. The NaOH solution was titrated against HCl acid in the presence of the Phenolphthalein indicator to determine the NaOH quantity that absorbed CO₂. The root respiration rate was regularly estimated every 10 days.

2.3.3. Leaf Relative Chlorophyll Content (LRCC)

Leaf relative chlorophyll content (LRCC) (greenness degree) was measured as SPAD units using SPAD-502 chlorophyllmeter device; Konica Minolta Sensing, Inc., Osaka, Japan. The 4th leaf from the main stem tip was subjected to measure the LRCC. The data of the LRCC was collected on attached ten leaves on different plants. This measurement was collected 4 times, began after 5 weeks of planting then repeated every two weeks along the growing season.

2.3.4. Leaf Area (LA)

After 65 days from planting the leaf area (LA) was measured. Ten leaves from different 10 plants (4th leaf from main stem tip) for each experimental plot were detached then immediately transferred to the lab. Ten leaf disks were brought from the top leaflet of the leaf using a cork borer. The leaf and disks were weighed then the average leaf area in cm² was calculated based on the relationship between discs area and its weight and leaf weight as described by Koller [20].

2.3.5. Leaf Dry Weight

After 65 days from planting the leaf dry weight was measured as an average weight of ten leaves collected from different 10 plants per each experimental plot. The chosen leaves were represented the 4th leaf from the main stem tip. The leaves were placed in paper bags then dried at 70c till the weight was constant thus calculate the leaf dry weight.

2.3.6. Nutrient Analysis

Nitrogen, phosphorus, potassium and calcium content of leaf were measured in the dry leaves in the digested extract. The digested extract was prepared using sulphuric-perchloric acid method according to Cresser and Parsons [21]. Leaf nitrogen content was measured using the method of Kjeldahl digestion described by Muñoz-Huerta, et al. [22]. Phosphorus content in the leaf was measured using an ascorbic colorimetric method described by Murphy and Riley [23]. Potassium and calcium were measured in the leaf digested aqueous extract using the flame photometer method described by Bovay and Cossy [24].

2.3.7. Leaf Relative Water Content (LRWC) and Leaf Relative Water Deficit (LRWD)

The LRWC was measured using six leaf discs (2 cm in diameter) according to the method described by Tourneux, et al. [25]. To measuring the LRWC, the leaves were sampled twice per day, early in the day at 6:00 to 7:30 a.m. and in the mid-day, at 1:00 to 12:30 p.m. The LRWC was measured 3 times along the growing season. The LRWD was calculated as a percentage by subtracting the value of the LRWC from the number 100 according to the method of Barr and Weatherley [26].

2.3.8. Leaf Osmotic Potential (Mpa)

Leaf osmotic potential (Mpa) was measured on the cell sap of 6 terminal leaflets, collected from different leaves and different plants, using the osmometer as described by Shackel [27].

2.3.9. Catalase Enzyme (CAT) Activity

After 65 days from planting, ten of the terminal leaflets from different leaves from different plants were sampled for biochemical analysis. The samples were analyzed immediately for CAT (EC 1.11.1.6) activity using the method described by Kumar and Knowles [28].

2.3.10. Proline Content

Proline content was colorimetrically measured in dried leaflets following the method of Chinard [29] that displayed by Abraham, et al. [30].

2.3.11. Soluble Carbohydrates Content

Soluble carbohydrates content in leaflets were assayed using lyophilized tissue which ground with mortar and pestle and extracted three times with 80% ethanol. The ethanol extract was evaporated to dryness in vacuo. The residues were resuspended in warm water then filtered to obtain solutions for total soluble sugars which were run with an anthrone assay [31]. The resulting glucose was assayed calorimetrically using glucose oxidase [32].

2.3.12. Measurements on Tuber and Tuber Yield

Potato tubers were harvested, after 106 or 107 days from planting in the 1st and 2nd seasons, respectively, where the haulm became almost dry and tubers became fully mature. Ten plants from each experimental plot were chosen randomly so the haulm was removed and the tubers were harvested manually. The marketable tubers were counted to record the number of tubers per plant. The tubers were weighed to record the tuber yield per plant then divided by the tubers number to calculate the average tuber weight. The tuber yield per hectare was estimated by multiplying the value of tuber yield per plant by plant number per hectare (average 60,000 plants based on the plants' density applied in the experiment).

Water Productivity or water use efficiency is a measure of the economic grain yield is produced from the use of a unit of water consumed in crop production. Water productivity

was calculated as the number of kilograms tubers produced per cubic meter of irrigation water according to the following equation [33].

$$\text{Water productivity (kgm}^{-3}\text{)} = \frac{\text{Grain Yield (kg ha}^{-1}\text{)}}{\text{Irrigation Water Applied (m}^3\text{ha}^{-1}\text{)}}$$

The consumed amount of irrigation water was calculated for irrigation of one hectare of potatoes was 3220 m³ and 4600 m³ when applied with the irrigation treatments of deficit and optimum irrigation, respectively.

2.4. Statistical Analysis

Analysis of variance was carried out on all the data variables using SAS software (Cary, CA, USA). Duncan's multiple range test was applied for the distinction between means.

3. Results

3.1. Analysis of Variance (ANOVA) Procedure Considering H₂O₂ Application with Irrigation Level on Potato Plants

Analysis of variance (ANOVA; Table 4) showed that all growth parameters except number of branches, root respiration, N, P, K, Ca, leaf relative water content, leaf relative water deficit, leaf osmotic potential, proline, total carbohydrates, catalase (CAT), tuber yield and water use efficiency were significantly responded to the application of H₂O₂ with irrigation.

Table 4. Analysis of variance (ANOVA) results of potato plant traits affected by hydrogen peroxide injection under deficit and optimum irrigation regime.

Trait	D _f	Mean Square	F-Value	p-Value
Branches number	5	0.4888889	0.5246 ns	0.0618 ns
Stem length	5	113.99647	53.396328	0.0000 ***
Shoot dry weight	5	96.660173	44.827823	0.0000 ***
Leaf chlorophyll reading	5	20.373142	17.662396	0.0001 ***
Leaf dry weight	5	0.38621	69.535184	0.0000 ***
Leaf area	5	550.09037	72.896609	0.0000 ***
Root Dry Weight	5	4.0805433	24.369697	0.0000 ***
Root to Shoot ratio	5	0.0007021	17.674965	0.0001 ***
Root Respiration	5	10.378019	29.256672	0.0000 ***
Nitrogen cont. %	5	0.51705	203.83049	0.0000 ***
Phosphorus cont. %	5	0.0234161	14.341091	0.0003 ***
K cont. %	5	0.7247689	39.993378	0.0000 ***
Calcium cont. %	5	0.0056523	4.039521	0.0288 *
Leaf Relative Water Cont.	5	227.92749	130.07828	0.0000 ***
Leaf Relative Water Deficit	5	179.2018	158.90676	0.0000 ***
Leaf Osmotic Potential.	5	0.11945	14.311102	0.0003 ***
Leaf Proline Cont.	5	9.5617022	34.723668	0.0000 ***
Leaf Total Carbohydrates	5	59.783157	137.98024	0.0000 ***
Catalase activity	5	16.576276	45.765672	0.0000 ***
Tuber number/plant	5	6.1473789	29.013189	0.0000 ***
Average tuber weight	5	489.48241	84.385808	0.0000 ***
Tuber yield/plant	5	145942.99	66.534393	0.0000 ***
Tuber yield/hectare	5	525.42987	169.00871	0.0000 ***
Water productivity	5	20.350223	88.33329	0.0000 ***

* and *** indicate significant differences at $p < 0.05$, 0.01, and 0.001, respectively.

3.2. Effect of H₂O₂ Application (Irrigation) on Plant Growth, Biomass and Root Respiration

Potato plants were analyzed for vegetative growth in terms of length of the main stem, dry weight of each of the shoots and leaf, leaf area, and leaf relative chlorophyll content as

SPAD reading, which responded significantly to the hydrogen peroxide injection under deficit or optimum irrigation level (Figure 1). The plant response to hydrogen peroxide injection was different according to the irrigation levels. The least value of the mentioned parameters was recorded on the plants watered by deficit irrigation level without hydrogen peroxide injection compared to hydrogen peroxide injection at 300 and 600 ppm under the tested irrigation levels. Meanwhile, the highest values were obtained with both 300 and 600 ppm under optimum irrigation level. Injection of hydrogen peroxide (600 ppm) under deficit irrigation alleviated the inhibitory effects of drought stress on plant growth. Root dry weight and root to shoot ratio were affected by the tested irrigation levels and hydrogen peroxide injection rate in the same manner. However, the significant differences were obscure when hydrogen peroxide was injected by 600 ppm with a deficit irrigation level and injection of both 300 ppm and 600 ppm with the optimum irrigation level. H_2O_2 -supplemented irrigation significantly improves root respiration under water deficit irrigation.

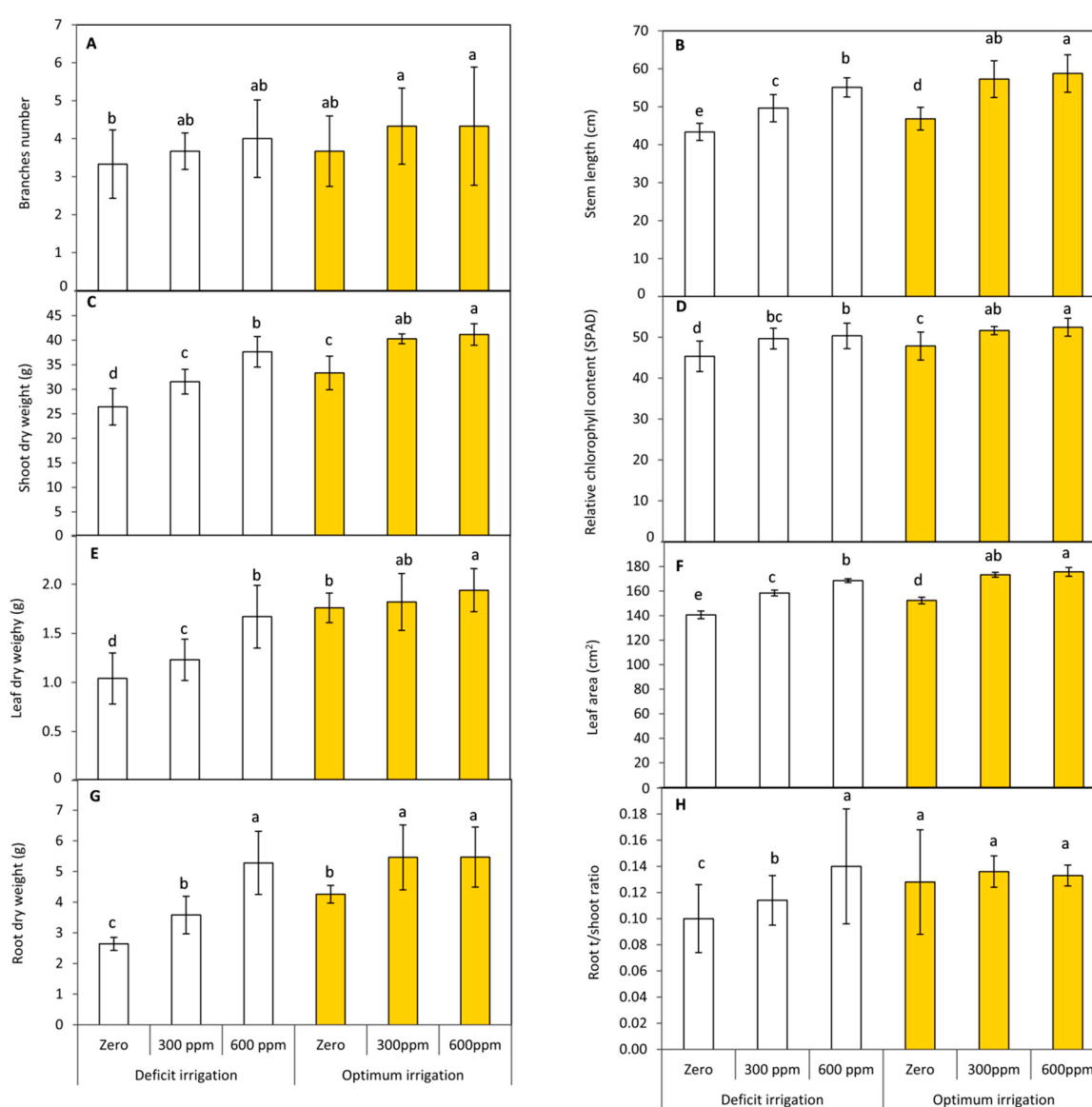


Figure 1. Effect of injection of hydrogen peroxide (H_2O_2) with irrigation water on branches number (A); stem length (B); shoot dry weight (C); relative chlorophyll content (D); leaf dry weight (E); leaf area (F); root dry weight (G) and root/shoot ratio (H) of potato plants grown under deficit and optimum irrigation levels in clay loam soil. Means followed by the same letters are not significantly different at $p \leq 0.05$ level; Duncan range test.

The measured root respiration rate of the potato plants was affected significantly by hydrogen peroxide injection under both deficit and optimum irrigation level (Figure 2). The recorded respiration rate values could be divided into 3 categories based on the significant variance of the data. The least root respiration rate was recorded in plants irrigated deficiently without hydrogen peroxide injection. The median root respiration rate was recorded in plants irrigated deficiently with an injection of 300 ppm of hydrogen peroxide and in other plants irrigated by the optimum irrigation level without hydrogen peroxide injection. The highest root respiration rate was recorded in plants irrigated by deficit level with an injection of 600 ppm hydrogen peroxide and in other plants irrigated by full level with an injection of 300 ppm and 600 ppm hydrogen peroxide.

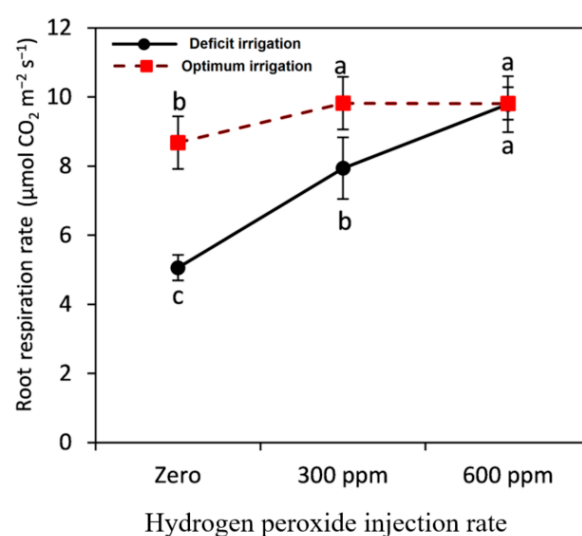


Figure 2. Effect of injection of hydrogen peroxide (H_2O_2) with irrigation water on root respiration rate ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) of potato plants grown under deficit and optimum irrigation levels in a clay loam soil. Means followed by the same letters are not significantly different at $p \leq 0.05$ level; Duncan range test.

3.3. Effect of H_2O_2 —Treatment (Irrigation) on Osmotic Status and Nutrient Acquisition in Potato Plants

3.3.1. Leaf Water Status (LWS)

The LWS is expressed by leaf relative water content (LRWC), leaf water deficit (LWD), and leaf osmotic potential (LOP). Leaf relative water content LRWC was significantly affected by hydrogen peroxide injection at 0, 300, and 600 ppm with either full or deficit irrigation level (Figure 3). The LRWC values were increased with increasing watering levels from deficit to optimum irrigation level but it increased with increasing the hydrogen peroxide injection rate only under deficit irrigation. The LWD showed inverse values for those of LRWC because the LWD represented the deficit water potential of the leaf meanwhile the LRWC represented the turgid water potential of the leaf. The LOP is a negative force of leaf cells result from increasing the concentration of the cell sap solutes where it helps in maintaining the leaf water content and/or boosts water transfer to the leaf. Treatment with hydrogen peroxide injection (600 ppm) under deficit irrigation resulted in higher LOP values in comparison with control (without hydrogen peroxide), treatment with lower concentration (300 ppm) or under optimum irrigation. However, the LOP values of optimum irrigated plants did not exhibit differences due to variable concentration of hydrogen peroxide injection

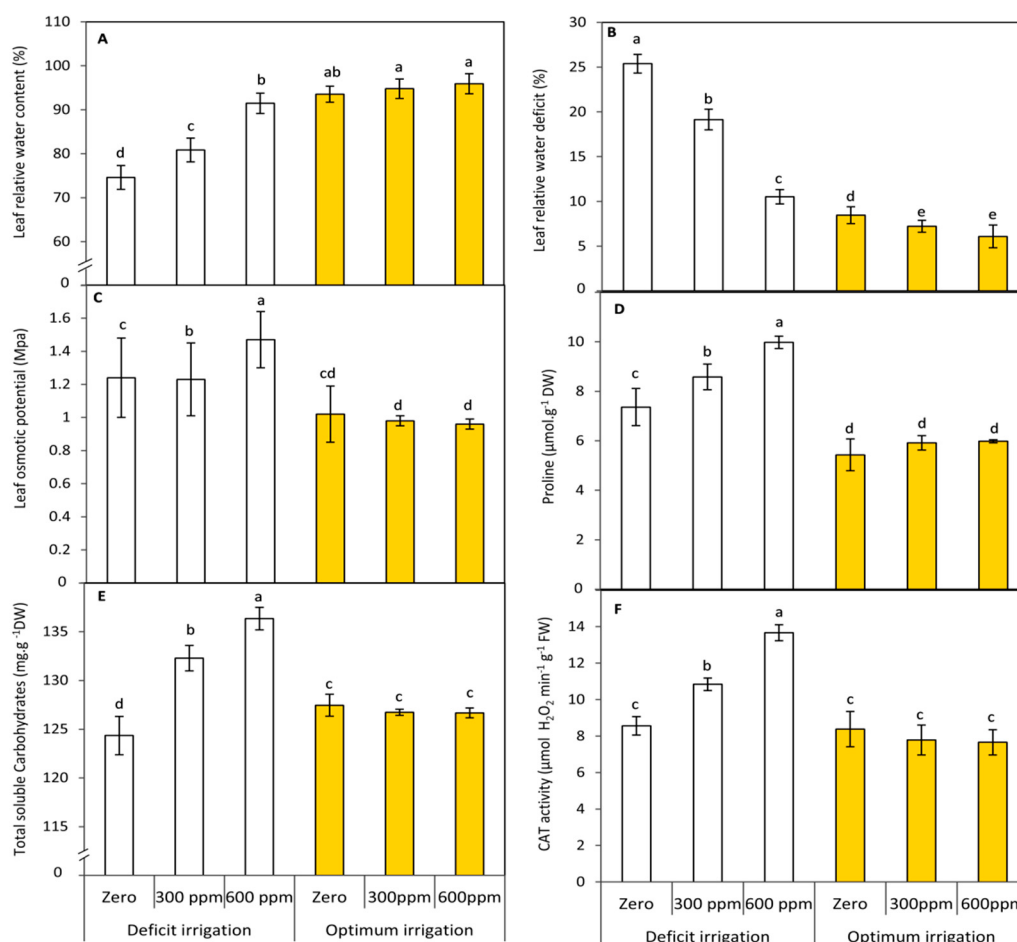


Figure 3. Effect of injection of hydrogen peroxide (H₂O₂) with irrigation water on leaf relative water content (A); leaf relative water deficit (B); leaf osmotic potential (C); proline (D); total soluble carbohydrates (E) and catalase activity (F) of potato plants under deficit and optimum irrigation levels clay loam soil. Means followed by the same letters are not significantly different at $p \leq 0.05$ level; Duncan range test.

3.3.2. Analysis of Osmolyte Content in Leaf

Analysis of proline and soluble carbohydrate content from leaves revealed the significant positive effects of hydrogen peroxide injection under deficit irrigation (Figure 3). The least values of both proline and soluble carbohydrates content in leaves were recorded in plants grown in optimum irrigation level in the absence or presence of hydrogen peroxide injection (300 ppm and 600 ppm).

3.3.3. Catalase (CAT) Enzyme Activity in Leaf

Catalase activity in potato leaves differed significantly with varying both irrigation levels and with the hydrogen peroxide injection rates (Figure 3). The highest significant value of the CAT activity was recorded in leaves of plants irrigated by deficit irrigation level combined with injection 600 ppm of hydrogen peroxide followed by those of plants injected by 300 ppm of hydrogen peroxide under the same irrigation level. The least significant values of the CAT activity were recorded in plants leaves irrigated by deficit level without hydrogen peroxide injection and other plants irrigated by full level with either injected or uninjected with hydrogen peroxide.

3.3.4. Nutrient Analysis

Nitrogen, phosphorus, potassium, and calcium percent in leaf were analyzed as an indicator of the nutritional status of the potato plant (Figure 4). The data proved that

these elements concentration in the leaf were responded significantly to the hydrogen peroxide injection rates of 0, 300, and 600 ppm, along with watering levels of deficit or full level. The least significant values of all elements were recorded in leaves of plants irrigated by deficit level without hydrogen peroxide injection but the highest values were recorded in leaves of plants irrigated by full level with hydrogen peroxide injection at either 300 ppm or 600 ppm. Otherwise under deficit irrigation, injection of 600 ppm hydrogen peroxide recorded the higher elements concentration compared to zero and 300 ppm. But with optimum irrigation, all hydrogen peroxide rates (300 and 600 ppm) were alike in improving the concentration of the elements in plant leaves.

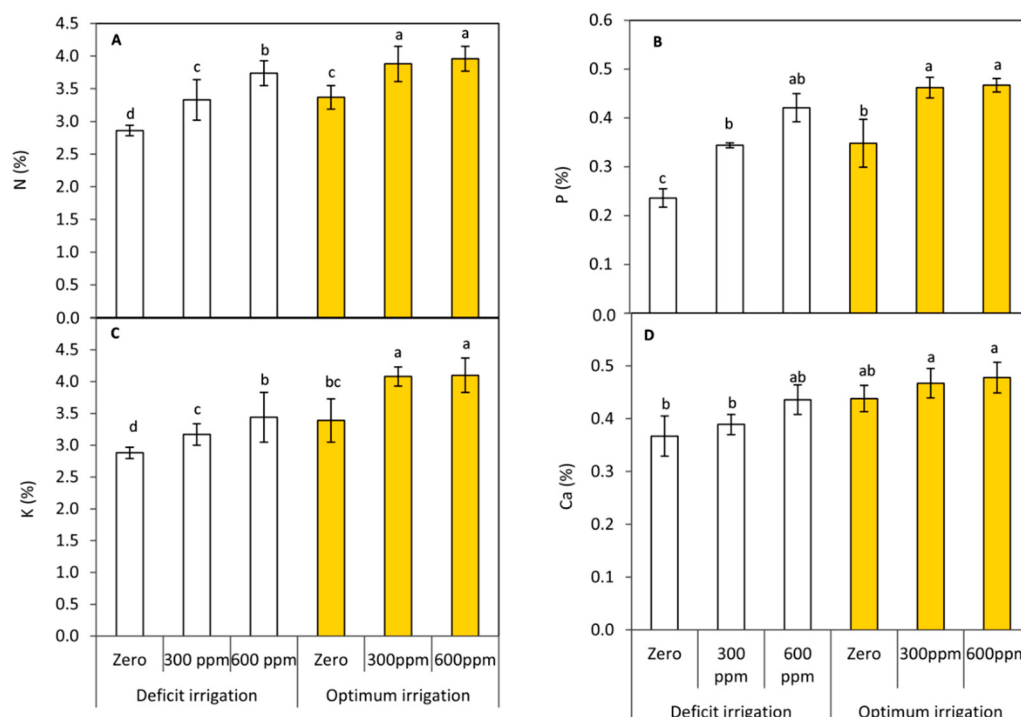


Figure 4. Effect of injection of hydrogen peroxide (H_2O_2) with irrigation water on the concentration of N (A); P (B); K (C) and Ca (D) of potato leaf under deficit and optimum irrigation levels clay loam soil. Means followed by the same letters are not significantly different at $p \leq 0.05$ level; Duncan range test.

3.4. Effect of H_2O_2 —Induced Oxygenated Irrigation on Yield Attributes and Water Use Efficiency in Potato

3.4.1. Yield Attributes

In the present work 600 ppm of hydrogen peroxide under deficit irrigation was observed to be most effective in providing optimum tuber yield per plant (Figure 5). Otherwise under deficit irrigation, injection 300 ppm of hydrogen peroxide improves tuber number compared to zero injection. The average tuber weight affected significantly by hydrogen peroxide injection either under deficit or optimum irrigation. Therefore the average tuber weight increased ascendingly with increasing hydrogen peroxide injection rate from zero to 600 ppm under deficit irrigation. The increment of average tuber weight during optimum irrigation is similar in two concentrations of hydrogen peroxide. Tuber yield per plant was estimated from multiplying the tuber number per plant by average tuber weight for each treatment.

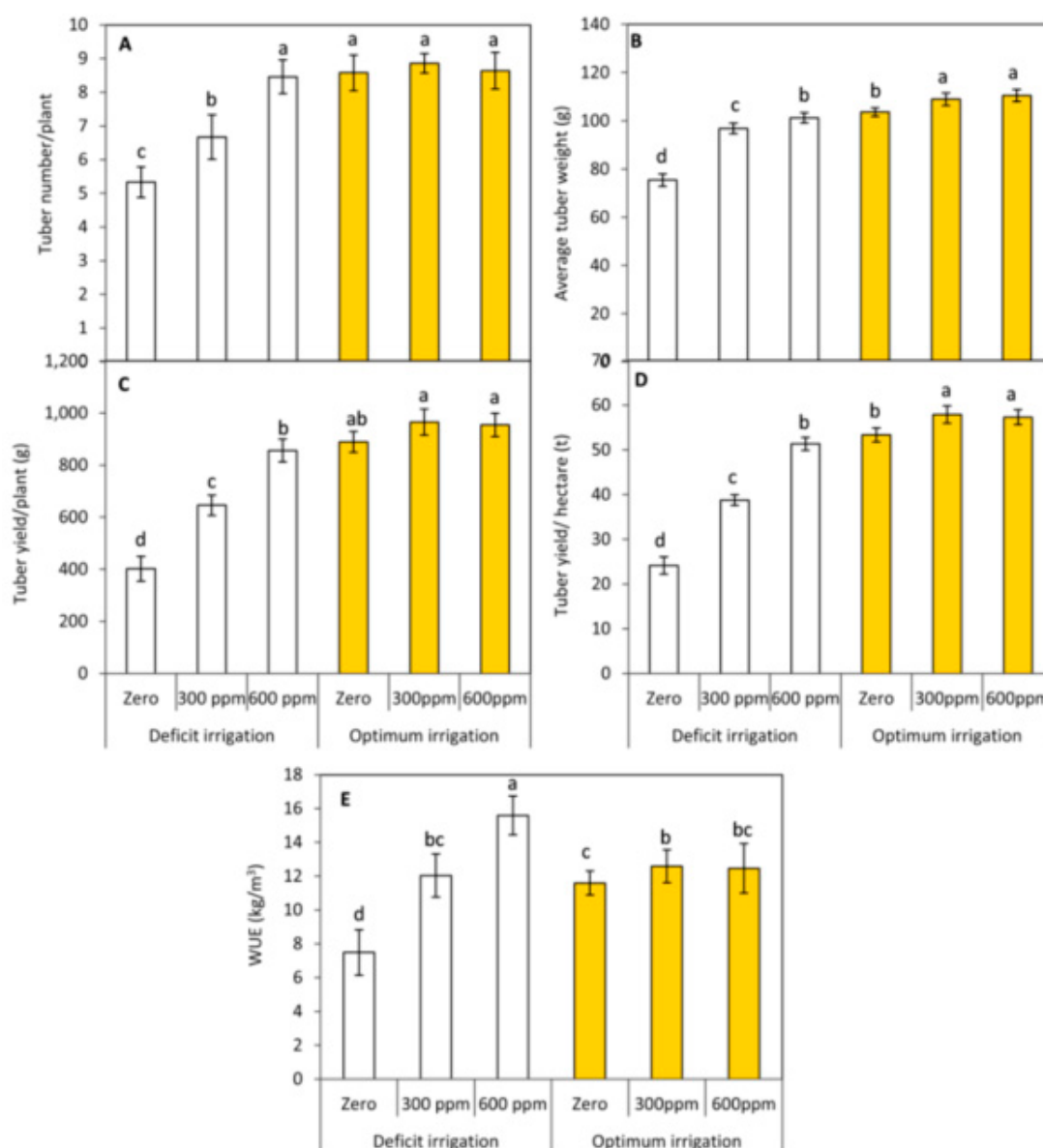


Figure 5. Effect of injection of hydrogen peroxide (H_2O_2) with irrigation water on tuber number. Plant⁻¹ (A); average tuber weight (B); tuber yield. plant⁻¹ (C); tuber yield .ha⁻¹ (D) and water use efficiency “WUE” (E) of potato plants under deficit and optimum irrigation levels in a clay loam soil. Means followed by the same letters are not significantly different at $p \leq 0.05$ level; Duncan range test.

3.4.2. Water Use Efficiency (WUE)

Water use efficiency is a criterion for comparing the economics of water units consumed in agriculture between different water treatments (Figure 5). The water productivity of potato plants were higher under deficit irrigation supplemented with hydrogen peroxide. The highest value of water productivity was recorded with the injection of hydrogen peroxide at 600 ppm under a deficit irrigation level. By contrast, the least value was got with deficit irrigation without hydrogen peroxide injection. Meanwhile, injection of hydrogen peroxide at 300, and 600 ppm under complete irrigation as well as injection of hydrogen peroxide at 300 ppm under deficit irrigation were alike but higher than both full and deficit irrigation without hydrogen peroxide injection.

4. Discussion

The present work demonstrates the role of H_2O_2 injection (300 and 600 ppm) in the improvement of plant growth, osmolyte accumulation nutrient acquisition and tuber yield of potato plants subjected to two irrigation regimes (deficit and optimum irrigation levels). In the present work deficit irrigation significantly reduced vegetative growth, tuber yield, and other physiological parameters compared to optimum irrigation conditions. Interestingly, the present report exhibits the effectiveness of H_2O_2 in circumventing oxygen deficiency during water deficit irrigation. The analysis of various growth and osmotic parameters (leaf area, tissue water content, root growth, root-shoot ratio) followed by measurement of biochemical attributes (nutrient acquisition, proline content, osmotic potential, and total soluble carbohydrate) indicate 600 ppm H_2O_2 to be most effective in mitigating stress during water-deficit irrigation.

Wang, et al. [34] reported that drought stress diminishes soil respiration under mesic and xeric ecosystems. Potato cultivation in mesic ecosystems leads to its susceptibility to over-wetting or waterlogging conditions. The available oxygen in the clay (soil of the experiment) or compacted soils is significantly low [35] thus intensifying the effect of anoxia and drought stress in potato plants. Therefore, the availability of enough oxygen in the soil via oxygenation of irrigation water by aeration and/or injection of oxygen-generating compounds can attenuate the deleterious effect of the stress [36].

In the current study, H_2O_2 injection significantly increased potato root dry weight and root to shoot ratio either under deficit or optimum irrigation level compared to zero H_2O_2 injection. H_2O_2 injection boosted the activity of root which was clear in rising soil respiration and enhancing root characters and activities triggered by increased absorption of water and nutrients and its transfer to the aerial parts. Investigations reveal the role of H_2O_2 in triggering adventitious rooting in the culture solution of sweet potato [37]. It was observed that 0.5 mM H_2O_2 was optimum in promoting adventitious rooting (root weight, root number, average root length), which, however, decreased at higher H_2O_2 concentrations (>5 mM). The authors analyzed the role of H_2O_2 in bringing about root elongation facilitated by the activity of peroxidase. However, higher concentrations of the treatment were likely responsible to create oxidative burst thus imparting inhibitory effect to root growth.

Earlier investigations reveal the effect of aeration and irrigation depth in modulating various yield attributes (fruit number, fruit size, lycopene content, sugar to acid ratio and total soluble solids) in tomato plants. Interestingly, 40 cm irrigation depth along with optimum aeration was found to be suitable to enhance the yield attributes [38]. Furthermore, H_2O_2 is known to improve fruit quality and plant growth. The optimum level of H_2O_2 is effective for improving fruit quality and its post-harvest storage [39]. In this investigation the authors also explain the role of H_2O_2 in maintaining the quality of flowers and the prevention of bud drop during chilling injury. In line with the earlier investigations, our present work reports the beneficial role of H_2O_2 (especially 600 ppm) in water deficit irrigation to be effective in improving plant growth and tuber yield. Monneveux, et al. [40] have reviewed several management strategies for developing drought-tolerant varieties of potato. Drought tolerance threshold of potato has been suggested to be measured by various parameters namely- stomatal conductance, biomass, leaf senescence, osmotic adjustment, root depth, tuber yield and water use efficiency. Since most of the modern varieties of potato are sensitive to drought stress it is necessary to analyze the wide genetic diversity of wild or native potato varieties. According to various investigations root architecture analysis, in situ root imaging, canopy temperature analysis and marker-assisted breeding are effective strategies towards drought tolerance analysis of potato cultivars. According to Monneveux, Ramírez and Pino [40], trait assessment methods adapted for cereals are also likely to be effective for drought management in potato varieties. Overexpression transgenics for various osmolyte biosynthesizing genes and transcription factors namely- dehydration responsive element binding factors, Basic Leucine Zipper Domain are suggested to be effective in raising drought tolerant potato varieties. Our

current findings provide substantial evidence to further investigate the role of hydrogen peroxide as a beneficial molecule for gene expression and metabolic regulation during drought stress in potato cultivars.

Deficit irrigation is often associated with reduced oxygen supply in the root zone which leads to reduced root growth and poor crop performance. Reports by Sariyev, et al. [41] refer to the use of H_2O_2 to be effective in mitigating adverse effects of soil compactness, reduced anoxia and improved crop yield in maize plants. In congruence to our present findings on the beneficial effect of H_2O_2 (300 and 600 ppm) in improving potato yield attributes, Sariyev, et al. [41] also reported that H_2O_2 injection in 100% and 70% FC irrigation to be effective in improving growth and grain yield in maize. Earlier investigations by Bhattarai, et al. [42,43] reported that H_2O_2 application in sub-surface drip irrigation is responsible for the improvement of fruit set, pod number, size and overall plant growth in zucchini, soybean and cotton. According to the authors, increased aeration in drip irrigation facilitates root growth and improves shoot-root ratio which in turn improves fruit set. In our present study, higher tuber yield is accompanied by the increased root-shoot ratio. Thus, improvement in the root system appears to be effective in regulating tuber yield in potato. Similarly, improved leaf area and increased leaf biomass indicate better translocation of organic solutes to the sink tissues i.e., tubers which, therefore, increases in average weight and numbers per plant. Present work also reveals improved nutrient acquisition (N, P, K, and Ca) in leaves of drought-stressed potato plants subjected to H_2O_2 treatment which possibly correlates with improved metabolism and tuber growth in potato. Increased proliferation of the root system is essential for optimum absorption of soil nutrients. H_2O_2 application in clay soil increased xylem diameter and xylem: phloem ratio in avocado trees [44]. Thus, based on the earlier supporting evidence, the present work reveals that H_2O_2 injection in clayey-loamy soil appears to be effective in combating water and anoxia stress. A summary of the present findings in well-watered and water deficit condition are explained in Figure 6.

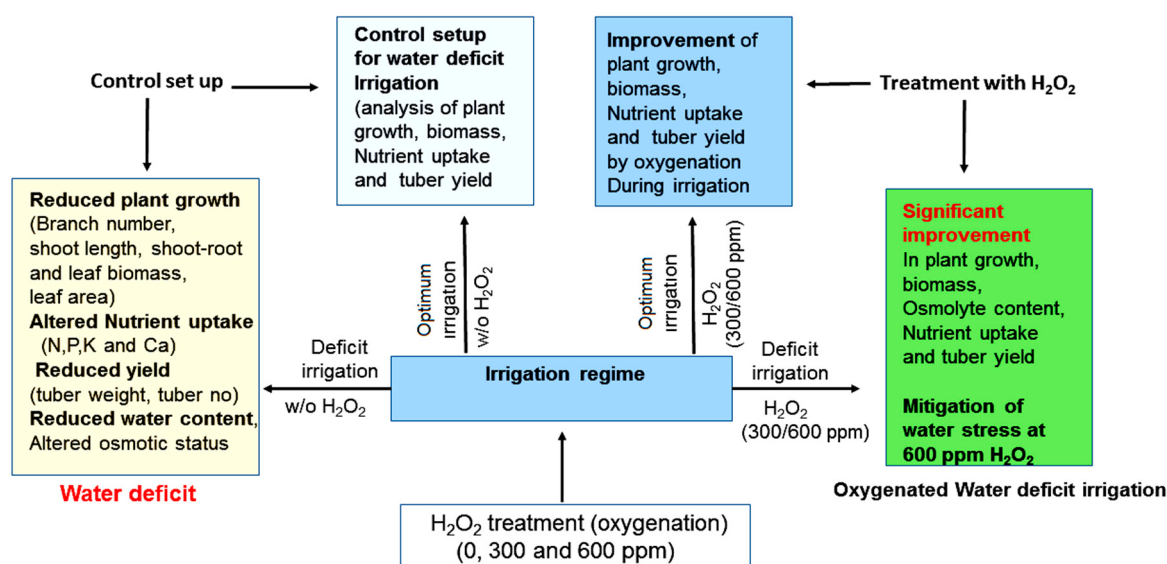


Figure 6. Effect of H_2O_2 (oxygenation; 300 and 600 ppm) supplementation under full and deficit irrigation regimes in the regulation of plant growth, biomass, nutrient uptake, osmolyte accumulation and tuber yield of potato. Effective oxygenation in water-deficit irrigation is achieved by 600 ppm H_2O_2 supplementation which results in mitigation of water stress evident by a significant improvement in plant growth, tuber yield and biochemical attributes.

Increasing root metabolic activity results in significant shoot growth manifested by an increase in the number of branches shoot dry weight, leaf dry weight, leaf area, and leaf nutrients content. On the other hand, H_2O_2 has a beneficial function when applied at low or normal concentrations ($1\text{--}5\text{ mM g}^{-1}\text{ FW}$), where it works as a messenger molecule

involved in adaptive signaling leading to various modes abiotic stresses tolerance [45,46]. For water productivity, Mazuela [47] concluded that adding potassium peroxide as oxygen releasing compound improved water use efficiency. A similar increase in water productivity was recorded in avocado by Gil, et al. [44] with H_2O_2 injection in the soil. Based on the aforementioned, it becomes clear that the lack of water supply due to deficit irrigation, especially in heavy soils, causes a lack of oxygen supply to the roots. Thus, in this investigation, the results prove that hydrogen peroxide injection improves all potato plant vegetative growth parameters either under full or deficit irrigation. Hydrogen peroxide injection under deficit irrigation alleviated the effect of drought stress accompanied by enhancement in root respiration. Available oxygen for root respiration from hydrogen peroxide injection encourages the production of enough ATP from sugars oxidation to maintain root health and enables it to carry out the physiological activities well [36]. Similar findings on maize were stated by Sariyev et al. [41] since found that adding H_2O_2 through irrigation water enhanced plant growth and grain yield parameters along with water use efficiency either at a deficit or optimum irrigation even if H_2O_2 concentration differed. However, in continuation to the present work further physiological investigations are required to decipher the correlation between hydrogen peroxide signaling and water use efficiency in drought-stressed plants.

5. Conclusions

Lack of oxygen in the soil and decrease of soil respiration are associated with deficit irrigation practice, especially in the heavy and compacted soils. Oxygenation of the irrigation water by H_2O_2 injection helps in saving oxygen for soil respiration and utilizes H_2O_2 as a beneficial signaling molecule. This is reflected in good growth, physiological events, and tuber yield production. Injection of H_2O_2 in irrigation water helps in adjusting the plant water status in terms of leaf relative water content, leaf water deficiency, and osmotic potential. Therefore, treating irrigation water by H_2O_2 enables the plant to surpass the deleterious effect of deficit irrigation. The applied H_2O_2 concentration, (600 ppm) was more efficient with deficit irrigation while 300 ppm of H_2O_2 seemed to be better efficient with optimum irrigation. To sum up, the present work attempts to analyze the role of H_2O_2 injection (oxygenated irrigation) in mitigating drought-stress in poorly aerated clay-loamy soil. Thus, it is evident that 600 ppm H_2O_2 appears to be optimum in improving vegetative growth, osmotic tolerance, and improve yield in water-deficit irrigation in potato plants. Future investigations are necessary to decipher the complex signaling routes of H_2O_2 which result in modulation of root architecture, improved nutrient balance, and improved osmotic tolerance.

Author Contributions: Conceptualization, S.A.A.E., H.G.A.E.-G., and N.A.E.-A.; methodology, S.A.A.E., H.G.A.E.-G., M.F.M.I., H.A.I., A.A.G., R.F. and N.A.E.-A.; software, M.F.M.I., S.M., A.E.; validation, S.A.A.E., H.G.A.E.-G., M.F.M.I., S.M., A.E., E.A., H.A.I. and N.A.E.-A.; formal analysis, S.A.A.E., H.G.A.E.-G., M.F.M.I., and N.A.E.-A.; investigation, S.M., A.E., E.A., H.A.I. and N.A.E.-A.; resources, S.A.A.E., A.E., E.A., H.A.I. and N.A.E.-A.; data curation, S.A.A.E., H.G.A.E.-G., A.A.G., R.F., M.F.M.I., and N.A.E.-A.; writing—original draft preparation, S.A.A.E., H.G.A.E.-G., M.F.M.I., S.M., and N.A.E.-A.; writing—review and editing, S.A.A.E., H.G.A.E.-G., M.F.M.I., S.M., A.E., E.A., H.A.I. and N.A.E.-A.; visualization, M.F.M.I., A.E., E.A.; supervision, S.A.A.E., M.F.M.I., S.M., A.E. and N.A.E.-A.; project administration, S.A.A.E., H.G.A.E.-G., M.F.M.I., S.M., A.E., E.A., H.A.I. A.A.G., R.F. and N.A.E.-A.; funding acquisition, S.A.A.E., A.E., E.A., H.A.I., A.A.G., R.F. and N.A.E.-A. All authors have read and agreed to the published version of the manuscript.

Funding: This research received no external funding.

Institutional Review Board Statement: Not applicable.

Informed Consent Statement: Not applicable.

Data Availability Statement: Not applicable.

Acknowledgments: We thank Taif University Researchers Supporting Project number (TURSP-2020/13), Taif University, Taif, Saudi Arabia.

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

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