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ORIGINAL PAPER

Intercropping the halophyte *Tetragonia decumbens* Mill. with salt-sensitive *Spinacia oleracea* L. mitigated salinity stress by enhancing the physiological, biochemical, and nutritional quality of the salt-sensitive species under saline cultivation

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Abstract

Increasing soil salinity is already having a significant effect on production losses of commercial vegetables around the globe. Thus, the implementation of innovative techniques is crucial to cultivate these vegetables amidst these unfavourable conditions. Halophytes are potential plants for resilient agricultural systems, such as intercropping with glycophytes, to enhance their productivity in saline soils. Therefore, the purpose of this study was to examine the intercropping potential of the halophyte *Tetragonia decumbens* in alleviating the damaging effects of salinity stress on spinach (*Spinacia oleracea*). Spinach seedlings were grown alone and in consociation with the halophyte under various salt stresses (50, 100, 150 and 200 mM NaCl). Results showed that increasing salinity reduced crop growth, relative water content, chlorophyll, and nutritional quality of spinach in monocultured system. Similarly, high salinity treatment induced severe oxidative stress depicted by high amounts of superoxide, malondialdehyde and the upregulation of superoxide dismutase, catalase, peroxidase, polyphenols, and flavonoids. Interestingly, intercropped spinach irrigated with 50 and 100 mM revealed a substantial enhancement in crop performance, reduction in oxidative stress and had improved nutritional quality depicted by high amounts of minerals, proximate constituents, and vitamins. These results support the introduction of *T. decumbens* in vegetable farming systems and highlights its positive impact on improving the overall crop performance of salt sensitive vegetables under saline condition.

Keywords Food security · Intercropping with halophytes · Phyto-desalination · Saline agriculture

1 Introduction

Global climate change and increasing soil salinity are already having a significant effect on production losses of commercial vegetables around the globe and will undoubtedly deteriorate food production in the coming years (Giordano et al. 2021; Shah et al. 2024). Salinity has been linked to the excessive utilisation of low-quality water, widespread irrigation, intensive agriculture, and insufficient drainage systems, leading to the accumulation of soluble salt ions in the soil (Hassani et al. 2020). These salt ions hinder the capacity of the roots to absorb water, causing osmotic stress and nutritional deficiencies that disrupt essential physiological processes such as photosynthesis, tissue hydration, and the onset of oxidative stress and membrane damage, ultimately leading to diminished plant biomass (Hussain et al. 2023; Mahmood et al. 2021). Thus, the application of innovative techniques is crucial to cultivate these vegetables in the mist of these unfavourable conditions. Phyto-desalination, an inexpensive plant-based bioremediation method, can drastically improve salt-affected soils through planting of appropriate salt extracting halophyte species (Trang et al. 2023; Zhang et al. 2023).

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Halophytes can be utilised as a cost-effective and eco-friendly method of phytoremediation to remove excess salt from salt-affected soils due to their reliance on osmotic adjustment, which involves the absorption of salt ions from the soil solutions of saline soils (Atzori et al. 2022). According to Jurado et al. (2024), intercropping with halophytes has been shown to significantly decrease sodium adsorption ratio, chloride content, and electrical conductivity at the soil level, resulting in a reduction in soil salinity. Similarly, Liang and Shi (2021) found that intercropping cotton with the halophyte *Suaeda salsa* L. enhanced the total above-ground biomass and seed cotton yield under saline conditions through halophyte root extraction of sodium ions in the soil. While Hu et al. (2020) noted an increase of vitamin C in cauliflower intercropped with salt tolerance grass under saline conditions. These findings suggest that intercropping halophytes with salt sensitive horticultural crops under saline conditions might alleviate the detrimental effects of salinity on crop production.

Tetragonia decumbens Mill. is an underutilised edible halophyte of South Africa (Nkcukankcuka et al. 2022). Recently, the species has been shown to extract and accumulate Na^+ and Cl^- in the leaf vacuole when cultivated under increasing salinity (Sogoni et al. 2023). Moreover, enhanced bladder cells such as peltate trichomes were noted in the leaves under scanning electron microscopy, suggesting that *T. decumbens* is a salt accumulator. Nevertheless, there are no reported studies on the phyto-desalination potential of this halophyte in an intercropping system under saline conditions. Thus, it became imperative to examine the intercropping potential of *T. decumbens* in alleviating the detrimental effects of salinity on plant growth, physiological, biochemical, and nutritional value of *Spinacia oleracea* "Beet Fordhook Giant" a widely consumed vegetable. Therefore, findings from this study are hoped to support the inclusion of this halophyte in vegetable farming systems and its adoption as a candidate species for phytoremediation in marginal arid and semi-arid regions affected by salinity.

2 Materials and methods

2.1 Greenhouse cultivation

2.1.1 Growth conditions

This study was conducted in the research greenhouse of the Cape peninsula University of Technology during October and November. The greenhouse was configured to have daytime temperatures of 21–26 °C and nighttime temperatures of 12–17 °C, with 60% relative humidity. Under natural light conditions, the daily average photosynthetic photon flux density (PPFD) was 420 μmol/m^{-2} s^{-1}, with the intensity peaking at 1020 μmol/m^{-2} s^{-1}. The photoperiod corresponds to the prevalent conditions of early spring to summer.

2.1.2 Preparation of plant materials and saline treatments

Seeds of salt sensitive *S. oleracea* were bought from a commercial garden store (Stodels™) and germinated on seedling trays following the procedure outlined by Yavuz et al. (2022) while the salt tolerant halophyte *Tetragonia decumbens* was propagated from stem cuttings using the technique described by Sogoni et al. (2022). Homogeneously established *S. oleracea* seedlings were transplanted individually (monoculture) and others were intercropped with *T. decumbens* in black plastic pots filled with a combination of peat and sand (1:1) and stationed in the hardening off area to acclimatize. The plants were then watered daily with a full Nutrifeed™ solution produced by STARKE AYRES Pty. Ltd., South Africa. After sixteen days of plant development, plants were irrigated with distilled water for six days to eliminate any salt residue before being subjected to saline treatments. Saline conditions were established on monoculture (*S. oleracea*) and on intercropping system (*S. oleracea* + *T. decumbens*) by gradually elevating the concentration of NaCl in the nutritive solution to formulate four treatments (50, 100, 150, and 200 mM) as described by Sogoni et al. (2021). These concentrations were chosen based on the salt tolerance limit of the chosen halophyte. The control (0 mM) plants were only irrigated with nutritive solution without salinity. Each pot received 300 mL of nutrient solution with or without the graded NaCl and were irrigated every two days. Drain water from each pot was collected and the electrical conductivity was measured to ensure that the right concentration of salinity in each pot was sustained. After two months of saline treatments, plants were harvested and used for further analysis.

2.2 Biomass yield assessment

After 60 days of plant growth under saline conditions, plants were thoroughly watered with distilled water to loosen up the soil and were harvested cautiously to prevent damage. They were then rinsed multiple times with distilled water and dried with tissue paper. Thereafter, the shoots and roots were separated with secateur, and the fresh samples were weighed using a laboratory scale, followed by oven-drying at 35 °C to complete dryness, and the dry samples were also weighed.

2.3 Physiological attributes

Photosynthetic leaf pigments: Chlorophyll a and b were estimated by spectrophotometric procedures by measuring the absorbance of the supernatants at 649 and 665 nm as explained by Wang et al. (2023). The variability in the leaf relative water content was evaluated following the procedure previously described by Bistgani et al. (2019).

2.4 Oxidative markers

Cell viability of the leaves was determined using the procedure described by Egbichi et al. (2014). The superoxide radical content was measured following the technique reported by Gokul et al. (2016) where the extinction coefficient of 12.8 mM cm^{-1} was used to calculate the superoxide radical levels. The malondialdehyde content of the tested samples was quantify using the procedure described by González-Orenga et al. (2021a, b).

2.5 Anti-oxidative enzymes

The method outlined by Gill et al. (2015) was utilised to extract protein from the tested leaf samples. The protein concentration in the extracts was measured using the Bio-Rad reagent and bovine serum albumin (BSA) as the standard. Spectrophotometric techniques were used to assess the activity of the selected antioxidant enzymes in protein extracts.

The activity of superoxide dismutase (SOD) was determined spectrophotometrically by measuring the suppression and photoreduction of nitro blue tetrazolium (NBT) at 560 nm. The NBT reaction solution uses riboflavin as a determinant of superoxide radicals. A unit SOD was labelled as the quantity of enzyme required to block NBT photoreduction by 50% in experimental conditions as outlined in the methodology of Brenes et al. (2020). Catalase (CAT) activity was measured by observing a decrease in absorbance at 240 nm following the consumption of H_2O_2 added to the extracts (Din Muhammad et al. 2024). One CAT unit was defined as the quantity of enzyme degrading one mmol of H_2O_2 at 25 °C per minute. While the enzyme activity of peroxidase (POD) was determined using the techniques and principles described by González-Orenga et al. (2021a, b).

2.6 Phytochemicals and antioxidant activity

The Folin-Ciocalteu technique described by Ingarfield et al. (2023) was utilised to evaluate the total phenolic content of the tested samples. Flavonol content was determined using the spectrophotometric aluminium chloride test reported by Cebani et al. (2024). The radical scavenging activity was determined using the DPPH free radical scavenging and Ferric Reducing Antioxidant Power (FRAP) assays following the methods described by Ngxabi et al. (2021).

2.7 Nutritional assessment

The mineral constituents (Macro and Micro-nutrients) of the tested samples were determined with the Inductively Coupled Plasma-Optical Emission Spectrometer (ICP-OES; Varian 710–ES series, SMM Instruments, Cape Town, South Africa). The proximate composition (moisture, ash, crude fat, crude protein, non-fibre carbohydrate and neutral detergent fibre) was determined using the accredited in-house standard Association of Official Analytical Chemists (AOAC) procedures reported by Tshayingwe et al. (2023). The composition of Vitamin A-retinol, Vitamin C-Ascorbic acid, and Vitamin E-α-tocopherol of the leaf samples were also evaluated using the AOAC methods described by Nemzer et al. (2021).

2.8 Anti-nutrients

The saponin content of the leaf samples was determined using the procedure explained by Jimoh et al. (2020), while oxalate was evaluated by a modified titration technique previously described by Adetunji et al. (2023).

2.9 Statistical analysis

The experimental data were analysed with Minitab statistical software and a multivariate analysis of variance was used to distinguish significant differences among treatments followed by Tukey's (LSD) test at $p \leq 0.05$. Prior to the analysis of variance, the validity of normality was evaluated by Shapiro–Wilk test, while Levene's test was used to examine the homogeneity of variance. The data were then expressed as mean ± standard error.

3 Results

3.1 Biomass yield assessment

Saline treatment had a considerable impact on the biomass yield of spinach grown in different cropping systems (Table 1). A significantly higher yield in shoot fresh weight was noted in plants subjected to 50 mM of salinity under intercropping system, however this was statistically similar to the yield obtained in control plants. A similar trend was also noted for shoot dry weight, where the maximum yield was again obtained in plants treated with 50 mM under intercropping system while the lowest shoot dry weight was obtained in plants subjected to 200 mM under monocultured system. On the contrary, both the root fresh weight and root dry weight were significantly higher in control plants as compared to both cropping systems. When assessing the total fresh weight, plants subjected to 50 mM under

Table 1 Biomass yield assessment of spinach grown in saline conditions under monoculture and intercropping system

Salinity	Shoot wet weight (g)	Shoot dry weight (g)	Root fresh weight (g)	Root dry weight (g)	Total fresh weight (g)	Total dry weight (g)
Control	213 ± 1.6ab	12.8 ± 04bcd	36.9 ± 1.6a	9.6 ± 1.1a	249.9 ± 1.2ab	22.4 ± 0.8b
M-50 mM	158.9 ± 1.2cde	12.5 ± 1.2bcd	16.3 ± 0.8bcd	4.2 ± 0.9 cd	175.3 ± 1.3cde	16.7 ± 1c
M-100 mM	139.02 ± 1.3def	9.8 ± 0.5d	14.2 ± 0.4 cd	5.2 ± 0.2bc	153.2 ± 0.9def	15.1 ± 0.4c
M-150 mM	115.3 ± 1.6ef	10.3 ± 0.8d	14.4 ± 0.8bcd	5.1 ± 0.3bc	129.8 ± 1ef	15.4 ± 0.9c
M-200 mM	93.74 ± 1.9f	8.8 ± 1.4d	10.2 ± 0.3d	1.8 ± 0.8d	104 ± 1.1f	10.7 ± 1.1d
I-50 mM	249 ± 1.3a	21.7 ± 1.3a	22.9 ± 0.7b	7.9 ± 0.6ab	272 ± 0.8a	29.6 ± 0.7a
I-100 mM	189.2 ± 0.9bc	16.2 ± 0.6bc	21.8 ± 0.6bc	4.4 ± 0.1 cd	211 ± 0.3bc	20.6 ± 0.9b
I-150 mM	175.1 ± 1.7bcd	16.8 ± 1.7b	17.9 ± 0.5bcd	3.3 ± 0.cd	193 ± 0.8bcd	20.1 ± 0.5b
I-200 mM	141.8 ± 1cdef	12.3 ± 0.6 cd	19.6 ± 0.9bc	3 ± 0.7 cd	161.4 ± 1cde	15.4 ± 0.3c

Means with different letters along the columns are significantly different at $P \leq 0.05$ (Tukey's Test). Data are means of thirty replicates per treatment (n = 30). Note: M = Monoculture, I = Intercropping

Table 2 Photosynthetic pigments and relative water content (RWC) of spinach leaves grown in saline conditions under monoculture and intercropping system

Salinity	Chl a (mg/ g FW)	Chl b (mg/ g FW)	Chl a + b (mg/ g FW)	Relative water content %
Control	6.8 ± 0.8a	4.1 ± 0.2a	10.9 ± 0.3a	90 ± 03a
M-50 mM	4.8 ± 0.5c	3.4 ± 0.6b	8.2 ± 0.8c	75.7 ± 1.1d
M-100 mM	4 ± 0.3e	2.1 ± 0.5d	6.1 ± 0.6e	68.7 ± 1.4e
M-150 mM	3.4 ± 0.2 g	1.8 ± 0.8e	5.3 ± 0.3f	66.8 ± 1f
M-200 mM	2.7 ± 0.4 h	0.9 ± 0.5 g	3.7 ± 0.3 g	65.2 ± 1.2 g
I-50 mM	6.7 ± 0.8a	4.1 ± 0.2a	10.8 ± 0.8a	88.6 ± 1.1b
I-100 mM	5.2 ± 0.3b	3.1 ± 0.2c	8.4 ± 0.4b	81.4 ± 1.2c
I-150 mM	4.4 ± 0.2d	2.1 ± 0.3d	6.5 ± 0.1d	75 ± 0.01d
I-200 mM	3.7 ± 0.6f	1.5 ± 0.1f	5.3 ± 0.5f	67.9 ± 0.5ef

Means with different letters along the columns are significantly different at $P \leq 0.05$ (Tukey's Test). Data are means of six replicates per treatment (n = 6). Note: M = Monoculture, I = Intercropping

intercropping system had the highest total fresh weight, but these values did not differ significantly to the control. The lowest values in total fresh weights were all obtained in plants subjected to increasing salinity under monocultured system. This trend was also noted for total dry weight, where significantly higher values were recorded in most plants under intercropping system. While the least values were noted in plants cultivated under mono cropping system.

3.2 Physiological traits

Salinity induced physiological changes in spinach leaves grown in different cropping systems (Table 2). The highest photosynthetic pigments (Chl a and b) were noted in the control, but these values were statistically similar to those recorded in plants subjected to 50 mM of salinity under intercropping system. Increasing salinity caused a significant reduction of photosynthetic pigments in plants subjected to mono cropping system as compared to those in intercropping system. As such, the least values were obtained in plants subjected to 150 and 200 mM under mono cropping system. When assessing the relative water content within treatments, the control plants had the highest relative water content, and this was significantly higher than all other treatments. Nevertheless, plants subjected to increasing salinity (50 and 100 mM) under intercropping system had significantly higher relative water content than all plants subjected to mono cropping system.

3.3 Oxidative stress markers

Salinity and cropping system had an influence on the accumulation of superoxide radicals and Malondialdehyde (MDA) within the leaves of spinach as displayed in Fig. 1. A significant increase in superoxide was noted in plants subjected to increasing salinity under mono cropping system. The highest content of superoxide was obtained in plants subjected to 200 mM of salinity under mono cropping system and was significantly higher than treatments. While the least value was obtained in control treatment followed by plants subjected to 50 and 100 mM under intercropping system. A similar trend was also noted for MDA, where the highest content was obtained in plants subjected to 200 mM under mono cropping system. The least value of MDA was again noted in control plants, but did not differ significantly to plants subjected to 50 and 100 mM under intercropping system respectively.

3.4 Antioxidant defence system

Increasing salinity stimulated the activation of antioxidative defence system in spinach under different cropping

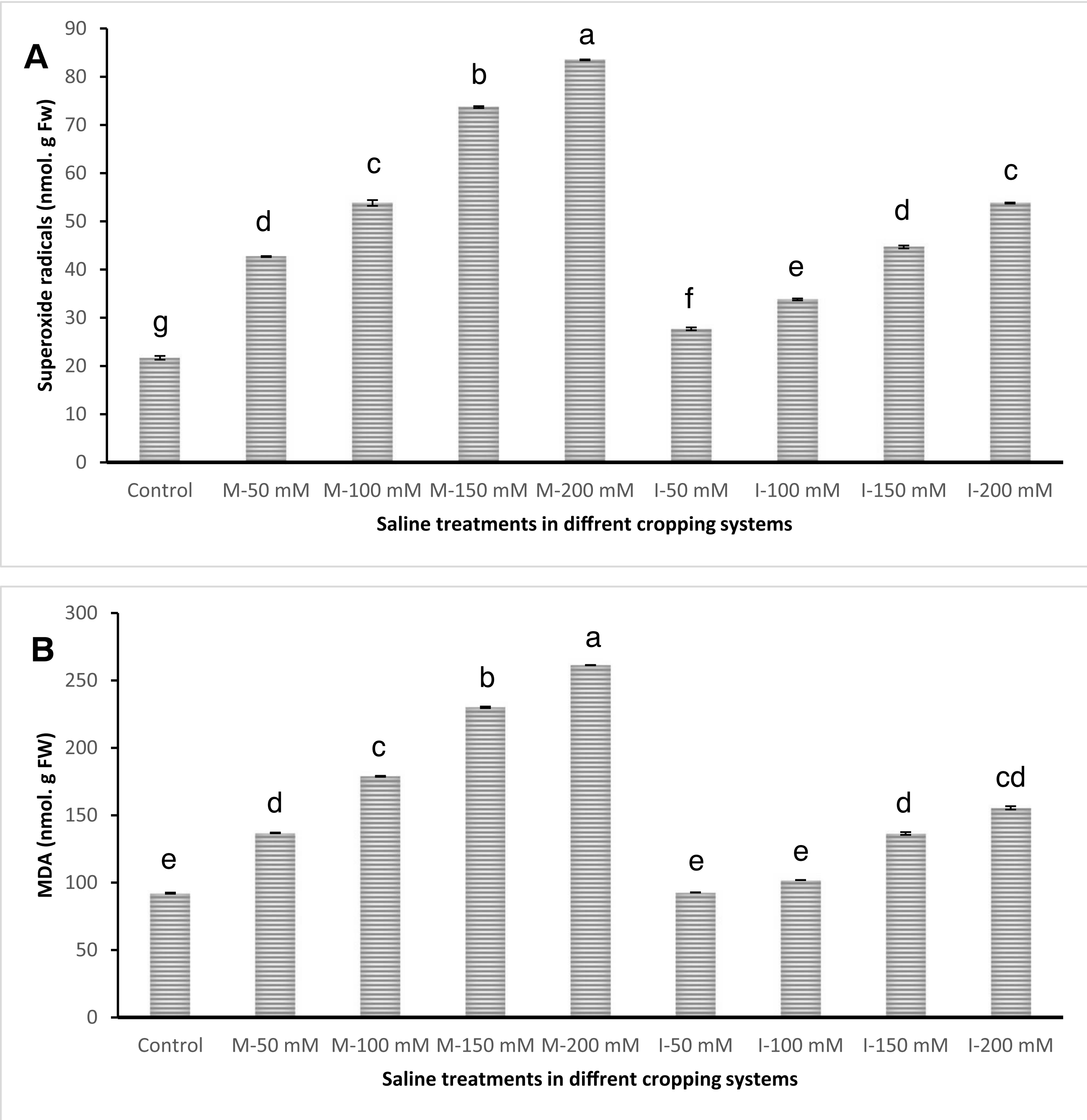

Fig. 1 Oxidative stress markers (A = superoxide and B = MDA) in spinach leaves grown in saline conditions under monoculture (M) and intercropping (I) system. Means with the different letters are significantly different at $P \leq 0.05$ (Tukey's Test). Data are means of six replicates per treatment (n = 6)

systems (Table 3). The antioxidative enzymes (SOD, CAT, and POD) were all enhanced with increasing salinity in plants subjected to mono cropping system. High amounts of SOD, CAT and POD were all obtained in plants irrigated with 200 mM of salinity under mono cropping system and these values were significantly higher than all treatments. While the least amounts were recorded in control, they were statistically similar to the values recorded in plants treated with 50 mM under intercropping system. A similar pattern was also observed when assessing the phytochemicals and antioxidant activity of the leaf samples, where the highest polyphenols, flavonols, FRAP and DPPH were all noted in plants irrigated with 150 and 200 mM of salinity under mono cropping system. Again, the least values were

Table 3 Antioxidant defence system of spinach leaves grown in saline conditions under monoculture and intercropping system

Salinity	Superoxide dismutase activity (U/ g^{-1} protein)	Catalase activity (U/ g^{-1} protein)	Peroxidase activity (U/ g^{-1} protein)	Polyphenols (mg GAE/g)	Flavonols (mg QE/g)	Ferric Reducing Antioxidant Power (µmol AAE/g)	DPPH (µmol TE/g)
Control	27.6 ± 1.4e	9.7 ± 0.4f	13.4 ± 0.4f	5.2 ± 0.4c	0.9 ± 0.04e	27.9 ± 0.9f	3.6 ± 0.5d
M-50 mM	38 ± 0.9 cd	14.2 ± 0.1d	16.5 ± 0.1d	6.9 ± 0.1a	1.1 ± 0.04d	36.2 ± 0.5d	18.4 ± 0.3ab
M-100 mM	41.3 ± 0.6c	17.3 ± 0.3c	18.2 ± 0.6c	7 ± 0.6a	1.2 ± 0.03c	39.7 ± 0.2c	14.2 ± 0.3bc
M-150 mM	59.3 ± 0.8b	19.2 ± 0.6b	20.4 ± 0.2b	7.2 ± 0.2a	1.4 ± 0.01b	45.9 ± 1b	17.4 ± 0.1ab
M-200 mM	76 ± 0.7a	21 ± 0.9a	24.7 ± 0.5a	7.3 ± 0.1a	1.5 ± 0.06a	50.6 ± 0.9a	22.9 ± 0.9a
I-50 mM	28.6 ± 0.6e	10.1 ± 0.5ef	13.8 ± 0.3f	5.4 ± 0.3c	0.9 ± 0.02e	26.8 ± 0.5f	4.4 ± 0.1d
I-100 mM	31 ± 0.4e	11.4 ± 0.2e	15.2 ± 0.2e	5.4 ± 0.2c	1 ± 0.01d	31.3 ± 0.8e	5.4 ± 0.6d
I-150 mM	37 ± 0.8d	15.3 ± 0.3d	16.7 ± 0.3d	6.2 ± 0.3b	1.1 ± 0.04d	39.7 ± 0.2c	11.5 ± 0.5c
I-200 mM	57 ± 0.5b	18.9 ± 0.1bc	18.4 ± 0.1c	6.4 ± 0.1b	1.5 ± 0.6a	45.8 ± 1.2b	17.1 ± 0.8bc

Means with the different letters along the columns are significantly different at $P \leq 0.05$ (Tukey's Test). Data are means of six replicates per treatment (n = 6). Note: M = Monoculture, I = Intercropping

obtained in control but did not significantly to the plants subjected to 50 mM under intercropping system.

3.5 Nutritional assessment

3.5.1 Minerals and vitamins

Saline treatment had a significant effect on minerals and vitamin content of spinach leaves under different cropping systems as shown in Tables 4 and 5 respectively. A significantly higher amount of nitrogen was obtained in control plants. Interestingly, higher phosphorus was noted in plants grown under intercropping system with a pronounce accumulation in plants subjected to 200 mM. When examining the accumulation of potassium and magnesium, the control plants had the highest amount, but these were statistically similar to the values obtained in plants treated with 50 mM under intercropping system. Nevertheless, increasing saline irrigation enhanced the accumulation of sodium in mono cropping system, with the highest value attained in plants subjected to 200 mM. The lowest sodium content was attained in control followed by plants subjected to intercropping system. Conversely, the calcium content was significantly higher in control plants followed by intercropped plants subjected to 50 mM.

Saline treatment also had a significant effect on the accumulation of micro-nutrients and vitamins in the leaves of spinach under different cropping systems. Zinc, Manganese, copper and iron were all reduced with increasing salinity under mono cropping system, while they were gradually enhanced under intercropping system. The highest yield of Zn, Mn and Fe were all noted in plants subjected to 100 mM under intercropping and these values were significantly different from all other treatments including the control. Nevertheless, Copper, vitamin C and vitamin A were more pronounced in control plants, however the vitamin C content was statistically similar to the plants subjected to 50 mM under intercropping system.

Table 4 Macronutrient composition of spinach leaves grown in saline conditions under monoculture and intercropping system

Salinity	N (mg/100 g)	P (mg/100 g)	K (mg/100 g)	Mg (mg/100 g)	Na (mg/100 g)	Ca (mg/100 g)
Control	4208 ± 15a	615 ± 11e	6845 ± 11a	775 ± 2a	4629 ± 14i	527 ± 8a
M-50 mM	3756 ± 6b	525 ± 12f	6558 ± 16b	725 ± 5b	5649 ± 9 g	375 ± 13d
M-100 mM	3754 ± 9b	489 ± 6 g	5459 ± 9c	705 ± 18c	6970 ± 11c	295 ± 6f
M-150 mM	3593 ± 11c	449 ± 9 h	4859 ± 11d	639 ± 14d	7958 ± 14b	265 ± 5 g
M-200 mM	3505 ± 8e	405 ± 12i	4125 ± 9e	511 ± 9e	8210 ± 12a	240 ± 10 h
I-50 mM	3116 ± 13 g	665 ± 18d	6640 ± 19ab	765 ± 15a	4865 ± 15 h	459 ± 8b
I-100 mM	3114 ± 16 g	837 ± 15b	6558 ± 11b	725 ± 5b	6385 ± 11f	405 ± 10c
I-150 mM	3528 ± 8d	785 ± 11c	5459 ± 9c	725 ± 15b	6490 ± 13e	345 ± 6e
I-200 mM	3399 ± 13f	880 ± 19a	5070 ± 15d	705 ± 18c	6650 ± 19d	235 ± 7 h

Means with different letters along the columns are significantly different at $P \leq 0.05$ (Tukey's Test). Data are means of six replicates per treatment (n = 6)

Table 5 Micronutrients and vitamin composition of spinach leaves grown in saline conditions under monoculture and intercropping system

Salinity	Zn (mg/100 g)	Mn (mg/100 g)	Cu (mg/100 g)	Fe (mg/100 g)	Vitamin C (mg/100 g)	Vitamin E (µg/100 g)
Control	9.5 ± 0.5b	11.3 ± 0.5 g	0.3 ± 0.0a	44.1 ± 0.9 g	51.8 ± 0.1a	15.2 ± 0.5a
M-50 mM	6.2 ± 0.1e	11.8 ± 0.2f	0.1 ± 0.0c	38.7 ± 0.4i	40 ± 0.1c	8.8 ± 0.9d
M-100 mM	6.7 ± 0.5d	12.8 ± 0.3e	0.0 ± 0.0e	42.2 ± 0.8 h	35.4 ± 0.5d	5.5 ± 0.2 g
M-150 mM	6.1 ± 0.2e	12.9 ± 0.2e	0.0 ± 0.0e	70.7 ± 0.7d	30 ± 0.01e	4.2 ± 0.6 h
M-200 mM	5.5 ± 0.1f	12 ± 0.3f	0.0 ± 0.0e	72.9 ± 0.7c	20.5 ± 0.5f	2.6 ± 0.1i
I-50 mM	9.4 ± 0.5b	16.9 ± 0.4d	0.2 ± 0.0b	45.9 ± 0.9f	52.1 ± 0.1a	15 ± 0.04b
I-100 mM	10.5 ± 0.6a	23.2 ± 0.8a	0.1 ± 0.0d	173.6 ± 0.9a	50.1 ± 1b	10.2 ± 0.5c
I-150 mM	9.5 ± 0.5b	20.2 ± 0.1b	0.1 ± 0.0d	120.7 ± 1.2b	40 ± 0.8c	8.3 ± 0.1e
I-200 mM	7.2 ± 0.1c	18.85 ± 0.8c	0.0 ± 0.0e	60.6 ± 0.6e	35.4 ± 0.9d	6.2 ± 0.05f

Means with different letters along the columns are significantly different at $P \leq 0.05$ (Tukey's Test). Data are means of six replicates per treatment (n = 6). Note: M = Monoculture, I = Intercropping

3.5.2 Proximate composition

The proximate composition varied significantly in the tested samples in both cropping systems under saline treatment (Table 6). The ash content was enhanced by increasing salinity with the highest yield recorded in plants subjected to 200 mM under mono cropping system. While the least value was noted in control plants. Conversely, crude fat was significantly higher in plants subjected to 50, 100 and 150 mM under intercropping system. The lowest values of fat were obtained in control and in mono cropping system respectively. Nevertheless, the protein content within the tested samples was found in abundant in control and this was significantly higher than all treatments. When assessing the moisture content of the samples, plants subjected to 50 and 100 mM under intercropping system had significantly higher moisture content than other treatments. Moreover, the non-fibre carbohydrate was significantly enhanced in control plants, while the neutral detergent fibre and Acid detergent fibre were substantially higher in plants subject to 200 mM under mono cropping system.

3.5.3 Anti-nutrients

Salinity and cropping system influenced the buildup of anti-nutrients in the leaves of spinach as shown in Fig. 2. A trend was noted, where increasing salinity significantly enhanced the accumulation of anti-nutrients with a pronounced effect in plants grown under mono cropping system. As a results, the highest yield of oxalate and saponin were all obtained in plants subjected to 200 mM of salinity under mono cropping system these values were significantly higher than all treatment including the control. While the least values were recorded in control and in plants subjected to 50, 100 and 150 mM under intercropping system.

Table 6 Proximate composition of spinach grown in saline conditions under monoculture and intercropping system

Salinity	Ash%	Crude fat%	Protein%	Moisture%	Non fibre carbohydrate%	Neutral detergent fibre%	Acid detergent fibre%
Control	34.2 ± 1.5i	1.6 ± 0.1e	26.3 ± 1.4a	6.3 ± 0.3b	32 ± 0.1a	32 ± 1.1d	21.4 ± 0.6 cd
M-50 mM	37.3 ± 1.1 g	1.9 ± 0.1d	19.4 ± 0.9f	6 ± 0.3d	29.4 ± 1.2c	31.3 ± 1.1f	18.3 ± 0.3e
M-100 mM	45.6 ± 0.8c	1.6 ± 0.1e	19.4 ± 1.3f	5.4 ± 0.1e	28.1 ± 1.6d	31 ± 0.9 g	20.7 ± 0.3 cd
M-150 mM	46.2 ± 1.1b	1.1 ± 0.0f	22 ± 1.1c	4.9 ± 0.2f	16.9 ± 0.7 h	34.8 ± 1.3b	24.5 ± 1.1b
M-200 mM	54.9 ± 1.1a	1.1 ± 0.0f	21.2 ± 1.9e	4.2 ± 0.7 g	1.3 ± 0.7i	42 ± 0.7a	34.7 ± 0.2a
I-50 mM	36.9 ± 1.1 h	2.8 ± 0.5a	23.4 ± 1.6b	7.1 ± 0.9a	30 ± 1.1b	30 ± 0.4 h	20.1 ± 0.9de
I-100 mM	38 ± 0.9f	2.3 ± 0.2b	23.4 ± 1.3b	7 ± 0.2a	19 ± 1.3 g	34.1 ± 0.2c	22.8 ± 0.2bc
I-150 mM	44.5 ± 1.5d	2 ± 0.5c	22.4 ± 1.1c	6.3 ± 0.2b	22.5 ± 1.2f	31.2 ± 1.1f	21.8 ± 0.9 cd
I-200 mM	44.1 ± 1.2e	1.6 ± 0.1e	21.9 ± 1.9d	6.2 ± 0.1c	23 ± 0.1e	31.6 ± 0.3e	20.7 ± 1.2 cd

Means with the different letters along the columns are significantly different at $P \leq 0.05$ (Tukey's Test). Data are means of six replicates per treatment (n = 6). Note: M = Monoculture, I = Intercropping

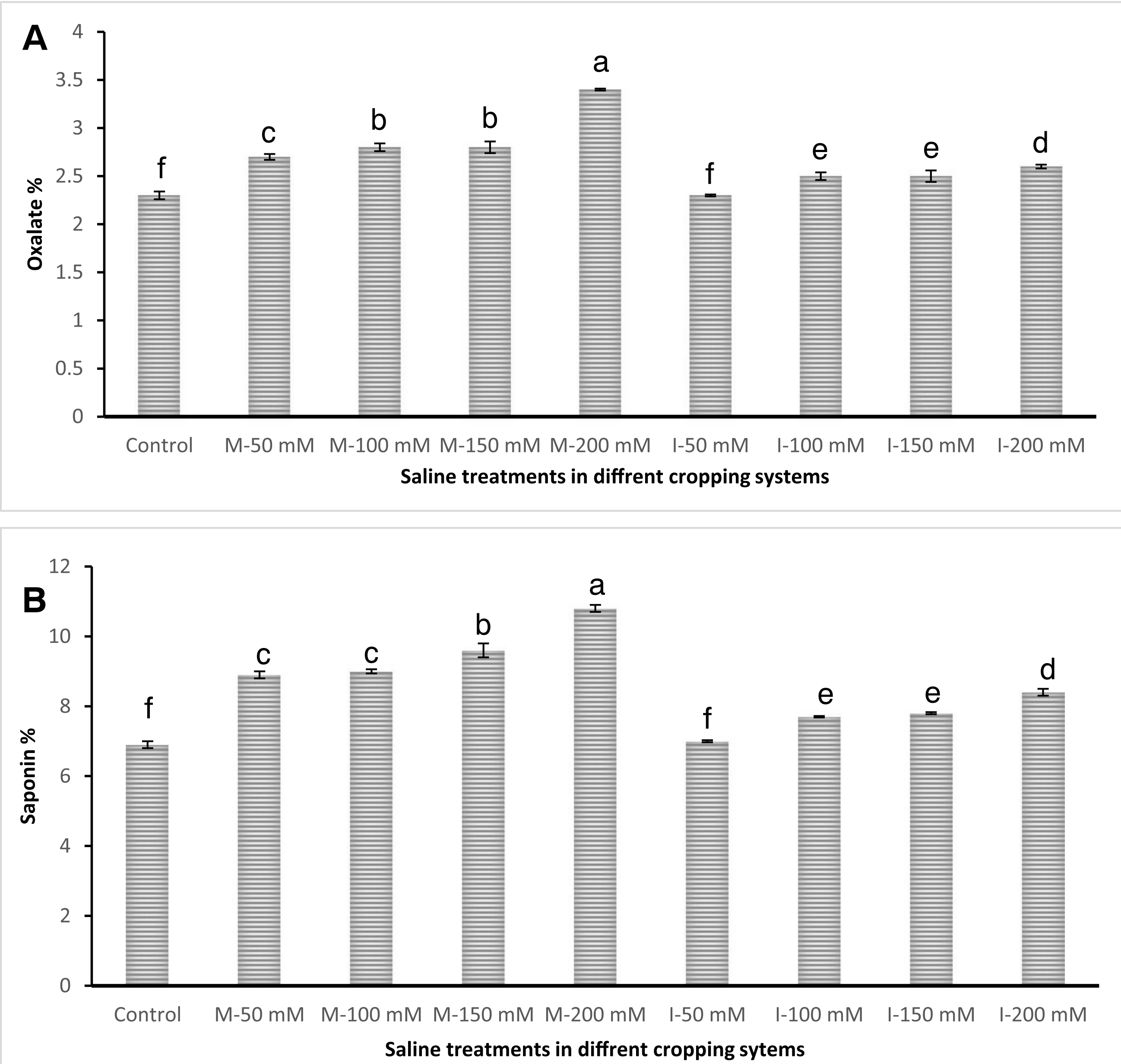

Fig. 2 Anti-nutrient composition (A = Oxalate and B = Saponin) of spinach leaves grown in saline conditions under monoculture (M) and intercropping (I) system. Means with the different letters are significantly different at $P \leq 0.05$ (Tukey's Test). Data are means of six replicates per treatment (n = 6)

4 Discussion

4.1 Intercropping system improved biomass yield

Salinity is a crucial environmental factor that hinders plants from achieving their full genetic potential (Balasubramaniam et al. 2023; Hussain et al. 2023; Lu et al. 2021; Singh 2022; Zarbakhsh and Shahsavar 2023). In addition, it hinders respiration, photosynthesis, and mineral absorption, leading to a decline in both crop yield and quality (Din Muhammad et al. 2024; Rasool et al. 2024). In the present study, the intercropping system using the halophyte *T. decumbens* improved the yield of spinach under low (50 mM) and moderate (150 mM) salinity levels compared to the mono cropping system (spinach only under saline conditions). This could be attributed to the salt accumulation and extraction ability of *T. decumbens* as reported by Sogoni et al. (2023) who showed through scanning electron microscopy that this halophyte utilises salt bladder cells such as peltate trichomes to store excessive Na^+ and Cl^- in the epidermal layer of the leaf. These results are supported by the findings of Liang and Shi (2021) on cotton plants where intercropping with the halophyte *Suaeda salsa* enhanced the total aboveground biomass and seed cotton yield under saline conditions through the root extraction of sodium ions in the soil. Similarly, Simpson et al. (2018) found that intercropping watermelon with the halophyte *Atriplex hortensis* substantially enhanced the yield and fruit quality of watermelon. Nevertheless, growth reduction in *Lactuca sativa* intercropped with the halophyte *Salsola soda* was also reported by Atzori et al. (2022), suggesting that not all halophytes can mitigate the detrimental effects of salinity when intercropped, some may outcompete the salt sensitive species for nutrients and light resulting in reduced growth. Hence specific halophyte selection as companion plants for horticultural crops still requires further studies under saline cultivation.

4.2 Cropping system induced changes in photosynthetic pigments and water relative content in response to salinity

The measurement of total chlorophyll content is often used as an indicator of salt tolerance in several plant species (Banakar et al. 2022), while relative water content is used as a suitable indicator of plant water level. Several plant species have shown reduced photosynthetic activity and relative water content when exposed to saline conditions mostly via a reduction in leaf area and the disruption of photosynthetic machinery (Khatri and Rathore 2022). In this study, the reduction in chlorophyll and relative water content in spinach treated with graded salinity under mono cropping system could be attributed to the disruption of photosynthetic machinery caused by the excessive build-up of sodium ions in the chloroplast. This affects the carbon metabolism and photophosphorylation resulting in reduced photosynthesis (Lawson and Vialet-Chabrand 2019). Similar reports of chlorophyll reduction in monocultured spinach and cowpea under increasing salinity were reported by Muchate et al. (2018) and Nanhapo et al. (2017) respectively. Nevertheless, spinach subjected to 50 mM under intercropping system had chlorophyll and relative water contents that were comparable to the control plants. This suggests that the uptake of sodium through osmotic adjustment and accumulation of compatible solutes in the chosen halophyte, played an important role in the absorption of water and nutrients by the roots of the intercropped spinach. Thus, maintaining a suitable chlorophyll and relative leaf water content is required for plant growth.

4.3 Generation of oxidative stress and antioxidant defence system

Various biotic and abiotic stimuli induce oxidative stress in plants by generating superoxide radicals via the Mehler reaction (Golldack et al. 2014; Rodrigues de Queiroz et al. 2023). Excessive production of these free radicals disrupts normal metabolic processes in the cytoplasm, mitochondria, and peroxisomes by causing oxidative harm to proteins and lipids. This leads to cellular dysfunction and, ultimately, cell death (Saleem et al. 2022). Various biochemical indicators, such as cell death, cell viability, superoxide, and lipid peroxidation, are often utilised to assess the level of oxidative stress in plants that are exposed to unfavourable environmental circumstances. The current study found that superoxide levels and lipid peroxidation increased in monocultured spinach, while there was a substantial decrease in intercropped plants treated with 50 and 100 mM of salinity. High production of free radicals with increasing salinity has been reported on numerous salt sensitive species (Manuel et al. 2017; Zulfiqar and Ashraf 2022). To curb this effect, plants activate the production of antioxidative enzymes and non-enzymatic compounds as a line of defence (Alfosea-Simón et al. 2020; Arif et al. 2020; Naz et al. 2016; Rahman et al. 2021). This was the case in this study where high amounts of antioxidative enzymes (SOD, CAT, and POD) and non-enzymatic compounds (Polyphenols and flavonols) were all produced in monocultured spinach to scavenge these highly toxic free radicals. Nonetheless, intercropped spinach had lower antioxidants suggesting the establishment of controlled oxidative stress within plant cells. These findings support earlier reports on the alleviation of salinity tolerance in salt sensitive species through halophyte intercropping (Jurado-Mañogil et al. 2023).

4.4 Impact of intercropping system on nutritional constituents

4.4.1 Minerals and vitamins

Salinity has been reported as a significant environmental element that impacts the ability of commercial vegetables to acquire nutrients. This is due to the alteration of ion transport and accumulation as a result of nutritional imbalances induced by Na^{+} and Cl^{-} ions competitors, which limit the uptake of essential nutrients required for optimal growth (Saddique et al. 2022; Vajjiravel et al. 2024). This was the case in this study, where an increase in sodium build-up in monocultured spinach leaves caused a significant decline in vital nutrients such as P, K, Ca, Mg and vitamin C and E. The observed outcome is a direct result of the antagonistic absorption of sodium and macro-cations by plants resulting in nutritional imbalances. This corroborates the findings of Neocleous et al. (2014), where increasing salinity caused a decline in essential minerals in green and red baby lettuce. Similarly, Ors and Suarez (2017) and Kim et al. (2021) also noted reduced minerals with increasing salinity treatment in spinach. Nonetheless, the intercropped spinach subjected to 50 and 100 mM of salinity had a balanced Na/K, Na/Ca and Na/Mg ratio which is a determining factor of counteracting the negative effects of salinity (Petretto et al. 2019). This could be attributed to the enhanced phytodesalinating capacity of *T. decumbens* as illustrated in supplementary data. Similar findings were also obtained by Jurado et al. (2024) and Karakas et al. (2021) on tomato and strawberry plants intercropped with halophytes under saline cultivation, where sodium ions were reduced drastically in leaves, thus maintaining a balance in nutrient composition required for growth. In addition, the intercropped spinach subjected to 50 and 100 mM also had an enhanced vitamin C and E. These findings correspond to those of Hu et al. (2020) on cauliflower intercropped with salt tolerance grass, where an increase in vitamin content was noted under saline conditions.

Moreover, intercropped spinach showed an increase in Zn, Mn, and Fe. This augmentation might have caused a positive impact on the response of spinach plants when subjected to salinity. Research has shown that supplementing plants with Zn and Mn enhances their performance in saline conditions by promoting plant growth through photosynthesis protection and reducing oxidative stress (Hasan et al. 2024; Khan et al. 2024; Ye et al. 2020). In this study, intercropped spinach exposed to 50 and 100 mM had the highest levels of Zn and Mn in their leaves, along with the highest levels of K^+, Ca^{2+}, and Mg. This may be connected to the higher crop productivity noted in these treatments which supports the idea that halophytes have a positive impact on improving plant mineral nutrition in *S. oleracea*.

4.4.2 Proximate and anti-nutrient composition

Nutritional value of commercial vegetables across the globe has been substantially affected by saline conditions, with a particularly noticeable effect in arid regions (Manuel et al. 2017). This has sparked worldwide interest in discovering strategies to sustain plant nutrition in the mist of salinity and to improve food security in impacted nations (Munir et al. 2022). In the present study, increasing salinity had an influence on the proximate composition of spinach subjected to different cropping systems. The highest ash, neutral detergent fibre (NDF) and acid detergent fibre (ADF) were all recorded in monocultured spinach. As salinity increases, plants absorb large quantities of sodium ions and subsequently translocate more into shoots leading to higher ash content (Nabati et al. 2014). Moreover, increasing salinity enhances the polysaccharides in cell walls and decrease soluble carbohydrates, thereby leading to increased insoluble fibres such as ADF and NDF (Hedayati-Firoozabadi et al. 2020). Interestingly, intercropped spinach had lower contents of ash, ADF and NDF respectively while the non-fibre carbohydrate content was increased in intercropped spinach subjected to 50 mM of salinity. This suggests that the intercropping system reduced the production of polysaccharides in the cell wall, thus increasing the yield of soluble carbohydrates in spinach.

Also, intercropped spinach had more protein and moisture content than the monocultured plants. These findings agree with the findings of Hedayati-Firoozabadi et al. (2020) on *Sorghum bicolor* intercropped with *Bassia indica* under saline conditions, where an increase in protein content was observed in intercropped samples, while reduced protein was reported in monocultured samples. The reduction in moisture content of monocultured plants can be linked to low amounts of minerals absorbed under saline stress (Kim et al. 2021). However, reduced protein could be attributed to the reduction in proteolysis synthesis as well as limited supply of amino acids and denaturation of enzymes involved in protein and amino acid synthesis (Athar et al. 2022).

Vegetables cultivated under saline conditions tend to possess high amounts of anti-nutrients such as oxalate and saponin which impair the uptake of nutrients or diminish their bioavailability (Barkla et al. 2024).

Various strategies such as soaking, steaming, and cooking have been documented to reduce anti-nutrients in plants (Caparrotta et al. 2019). In this study, increasing salinity enhanced the build-up of anti-nutrients in monocultured spinach, while they decreased in intercropped system. Hence, intercropping system can be harnessed to reduce the anti-nutrient composition of spinach when grown under saline treatment instead of boiling and steaming, which has been reported to reduce the vitamin constituents of the edible leaves (Badawy et al. 2018).

5 Conclusion

Salinity is one of the most critical concerns for agriculture in arid and semi-arid regions. This study shows that intercropping with the halophyte *Tetragonia decumbens* in control environment enhances growth, physiological, biochemical, and nutritional value of spinach plants irrigated with 50 and 100 mM of salinity. Nevertheless, high concentration of salinity prompted a mild oxidative stress in intercropped plants, which was reflected by a slight decline in plant growth. Nonetheless, this research supports the introduction of *T. decumbens* in vegetable farming systems and highlights its positive impact on improving the overall crop performance of spinach under saline condition. Furthermore, field studies in saline soils are recommended to broaden the mechanism of action and to ascertain the phytodesalinating potential of *T. decumbens*.

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Data availability Data is contained within the article.

Declarations

Conflict of interest The authors wish to declare no conflict of interest.

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