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ORIGINAL PAPER

Exploring the Effect of Nitrogen, Phosphorus and Potassium Rates of the Nutrient Solution on the Growth and Quality of Common Sowthistle (*Sonchus oleraceus* L.) Grown Hydroponically

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Abstract

Purpose Wild edible plants, including common sowthistle (*Sonchus oleraceus* L.), in modern diets presents a promising avenue for dietary diversification due to their specific nutritional profile with increased research interest and potential commercialization.

Methods This study evaluated the effect of different nitrogen (N) concentrations (100–200 mg L^{-1}; as N100, N200) in combination with different levels (decreased 0.66-fold, normal 1-fold, or increased 1.5-fold) of phosphorus (P; 47-70-105 mg L^{-1} as P47, P70, P105) and potassium (K; 250-350-525 mg L^{-1} as K250, K350, K525), incorporated in the nutrient solution (NS) for the cultivation of sowthistle in hydroponics.

Results Decreased (0.66-fold) or increased (1.5-fold) P and K levels, under N100 and N200 stimulated plant growth, chlorophylls and carotenoids. In addition, N100 in the NS increased (up to 16%) ascorbic acid content, whereas the combination of N100 and decreased or increased P and K levels resulted in increased (up to 45.5%) flavonoids. In the same P and K rates, phenols and antioxidant capacity were decreased, while N levels modulated this response. Hydrogen peroxide level increased (up to 58.7%) at $NPK_{200-70-350}$ application and coupled with decreases superoxide dismutase activity. Malondialdehyde levels increased (up to 36.1%) at $NPK_{200-47-250}$ application. Increased catalase and peroxidase activities were found in plants grown at $NPK_{100-105-525}$ application. Under the application of N100, the increased rates of P and K positively influenced N uptake, while the application of N200 led to an increase of P content.

Conclusions The modification of P and K in the NS, below or above the levels commonly applied in hydroponics for leafy vegetables, can lead to the stimulation of the growth and quality of sowthistle plants, with benefits to be observed under increased K and P levels at N100 treatment.

Keywords Soilless cultivation · Hydroponic · Sowthistle · Wild edible plants · Macronutrients

1 Introduction

While currently underutilized, wild edible plants (WEPs) represent a valuable part of the cultural and genetic identity of various regions, and are being consumed by over a 100 million people across the globe (Botella et al. 2024). Although declining, the consumption of WEPs offers a promising avenue for diversifying modern diets. Their unique nutritional profiles, which are rich in nutraceutical compounds, are vital for enhancing human health (Voutsinos-Frantzis et al. 2022). Recently, there has been a growing interest in utilizing such plant species in horticultural crop production, especially due to their adaptability to abiotic stress conditions. However, the lack of knowledge about cultivation methods for many underutilized species presents a significant barrier to their commercial adoption (Karkanis et al. 2024).

The *Sonchus* genus, belonging to the Asteraceae family, consists of more than 50 species that find wide distribution in Asia, Europe, and Africa. Species of the genus include *Sonchus arvensis*, *S. asper*, and *S. oleraceus*

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(Sánchez-Aguirre et al. 2024). Common sowthistle (*S. oleraceus* L.) an upright, annual herb composed of simple branches and smooth leaves. It is a widespread weed affecting crops, especially under extensive cultivation practices (Peerzada et al. 2019). Despite being considered as an invasive species, sowthistle has a range of culinary and medicinal uses. Its edible parts include the basal leaves and tender stems. Eaten raw in salads or cooked in stews, sowthistle is particularly rich in vitamins (C, A, K), minerals (P, K, Ca, Mg), antioxidants (flavonoids, carotenoids and phenols), making it a nutritious component of the Mediterranean diet (Botella et al. 2024). Its medicinal properties have also been documented, due to its antioxidant, anti-inflammatory, antidiabetic and hepatoprotective properties, reflecting its role in folk medicine. These benefits are due to its high content in polyphenols, flavonoids, and organic acids (Chrysargyris and Tzortzakis 2023; Sánchez-Aguirre et al. 2024). Despite this knowledge, sowthistle cultivation and commercialization has been limited. This is exacerbated by the limited research regarding its cultivation practices and nutrient requirements, thus preventing its commercial exploitation. Towards this end, recent research has focused on exploring the potential of sowthistle by evaluating its response under varying cultivation methods (e.g. hydroponics) and fertilization methods (e.g. organic fertilizers) (Chrysargyris and Tzortzakis 2023; Hajisolomou et al. 2024; Karkanis et al. 2024). However, the identification of optimal fertilization, especially in controlled settings, is still in preliminary stages.

Soilless cultivation, a technologically advanced agronomic practice mainly applied in greenhouses, has emerged as a promising approach to cultivating high-value crops, including underutilized and WEPs. Soilless cultivation offers a toolset for the manipulation of growth conditions, particularly through the management of the nutrient solution (NS) which serves as the source of all essential plant nutrients (Maggini et al. 2022; Trejo-Téllez and Gómez-Merino 2012). This high level of control allows for tailored nutrition management, extending beyond meeting basic growth demands, enabling the enhancement of specialized metabolites production (Alneyadi et al. 2024). These include bioactive compounds such as polyphenols and flavonoids, which contribute to the nutraceutical value of WEPs as functional foods. To achieve this, it is essential to maintain the nutrient concentrations of the NS within optimal ranges, to prevent nutrient imbalances (Fathidarehnijeh et al. 2024; Maggini et al. 2022). By optimizing growth conditions and manipulating the nutrient availability via the NS, soilless cultivation facilitates the efficient production of underutilized WEPs, addressing the demands of the modern society for high-quality and safe food sources (Ceccanti et al. 2018). Furthermore, soilless cultures, and particularly the utilization of closed hydroponic systems, presents a sustainable method of crop production, as it significantly reduces the consumption of water, and minimizes the discharge of nutrients in the environment (Chrysargyris and Tzortzakis 2023; Savvas and Gruda 2018).

The NS of soilless cultivation systems presents an aqueous solution composed of inorganic ions of essential elements for plants. Among the essential elements for plant nutrition, nitrogen (N), phosphorus (P) and potassium (K) have critical roles in numerous plant physiological and biochemical processes (Dordas 2008; Trejo-Téllez and Gómez-Merino 2012). Nitrogen has a central role in plant metabolism, acting as a constituent of proteins, chlorophyll, co-enzymes, phytohormones and secondary metabolites (Hawkesford et al. 2023). However, excess nitrogen fertilization can lead to imbalanced growth, thus reducing crop yield and nitrogen use efficiency (Chrysargyris and Tzortzakis 2023). Phosphorus is a major nutrient for plant growth and reproduction as it influences energy storage and transfer in plants (Fageria et al. 2011). Potassium is involved in a multitude of physiological and biochemical processes, including enzyme regulation, photosynthesis and carbon metabolism. It is a cofactor for over 50 enzymes, with its deficiency suspending their activities and ultimately inhibiting growth and development (Naciri et al. 2022). A balanced supply of N, P, and K positively influences the yield and quality of leafy vegetables such as lettuce (Hoque et al. 2010). The balance between N and K is also important as it influences plant growth, yield and quality. Furthermore, the N/K ratio is particularly important during the transition from the vegetative to the generative phase of plants, while a sufficient supply of K promotes N metabolism (Alvarado-Camarillo et al. 2018; Xu et al. 2020). Phosphorus concentration in the NS also plays a role in N accumulation and utilization. Conversely, N availability can influence the efficiency of P and K utilization (Bevan et al. 2021; Shah et al. 2024). In addition, the selection and comparison between ammonium (NH_4^+) and nitrate (NO_3^-) as sources of N has garnered increased attention, as it impacts the plants' physiology, morphology, and chemical composition (Zhu et al. 2014). In fact, Chrysargyris and Tzortzakis (2023) reported that a lower NH_4^+/total N ratio of 0.05 enhanced sowthistle yield and nutritional value, while higher rates resulted in the accumulation of P in plant tissues. However, the combined impact of N, P and K fertilization, especially on the systemic cultivation of sowthistle, has not been comprehensively investigated, highlighting a knowledge gap in this research topic.

Common sowthistle is presented as a WEPs with significant nutritional value. Despite this, sowthistle remains largely underutilized. Although a limited number of studies have been conducted, sowthistle demands further research to explore its potential as a sustainable and nutritious food

crop, and its commercial exploitation. Its introduction in hydroponic systems can provide an environment for achieving optimal growth and quality, while its nutrient requirements can be extensively examined. Understanding the interplay between nutrient uptake and growth of sowthistle, particularly under the influence of N, P and K rates, could contribute to maximizing its yield and nutritional quality. Thus, this study was commissioned to investigate the specific impact of varying N, P and K levels, as it was hypothesized that increased or decreased rates of P, and K can impact the unbalanced N rates and therefore the growth, yield, physiology, nutritional value and antioxidant status of sowthistle cultivated hydroponically. Therefore, this work aimed to establish optimal fertilization combinations and to contribute to a better understanding of the systemic cultivation of sowthistle.

2 Materials and methods

2.1 Cropping system, Plant Material and Growth Conditions

The experiment was carried out in a plastic multi-span greenhouse at the experimental farm of the Cyprus University of Technology, in Limassol, Cyprus. Greenhouse automation included a climate control system with passive and active ventilation. The greenhouse housed a hydroponic nutrient film technique (NFT) installation as described previously (Chrysargyris et al. 2024). Three hydroponic units were used as replicates for each tested treatment. The NS was replenished through automatic refill of water from the replenishment tank for each unit. Electrical conductivity (EC) and pH adjustments of the NS were conducted daily by the addition of appropriate amounts of stock solutions of fertilizers, as well as H_2SO_4 (5% *v/v*) for further pH control. The plants were spaced in 0.25 m among each other in each planting row which resulted in a plant density of 25 plants m^{-2}. Each hydroponic unit hosted 12 plants with a total 216 plants used in the current study.

Commercial sowthistle seeds were purchased from Greece (Geniki Phytotechniki Athinon SA, Athens, Greece) and were sown late winter 2022, in black plastic seedling trays containing a peat-perlite (85:15 *v/v*) based growing media (Professional peat, Gebr. Brill Substrate GmbH & Co.KG, Georgsdorf, Germany). Seedlings at the stage of the first true leaf were then transplanted into netted pots (11 days after sowing), filled with perlite and placed into the pot positions of the NFT channels, and were kept for one week under standard NS (sNS), to allow recovery from the transplanting stress. The nutrient concentrations in the sNS were as follows: NO_3^--*N* = 13.7, K^+ = 7.5, PO_4^{3-}-*P* = 1.8, Ca^{2+} = 3.5, Mg^{2+} = 1.0, SO_4^{2-}-S = 1.3 and Na^+ = 1.9 mmol L^{-1} respectively; and B = 30.0, Fe = 30.0, Mn = 5.0, Cu = 1.0, Zn = 4.0, Mo = 0.5, and Cl^- = 1.49 µmol L^{-1}, respectively.

After a plant acclimation period of 7 days, the modified NS was applied, as presented in Table S1 of the supplementary file. Specifically, two N concentrations (100–200 mg L^{-1}; as N100, N200) were examined, based on previous reports (Chrysargyris and Tzortzakis 2023), in conjunction with different levels (decreased 0.66-fold, normal 1-fold, or increased 1.5-fold) of phosphorus (P- 47-70-105 mg L^{-1} as P47, P70, P105) and potassium (K 250-350-525 mg L^{-1} as K250, K350, K525). The target pH and EC of the NS were 5.8 and 2.3 dS m^{-1} respectively. Plants were subjected to the different modified NS for a total of 15 days. Mean air temperature and humidity in the greenhouse were 24.1 °C and 56.6%, respectively, for the cultivation period.

2.2 Plant Growth and Tissue Analysis

Following 15 days of plant growth using the different NS, six individual plants obtained from different replication units for each treatment were used for plant height (cm), leaf number, shoot plant biomass and root fresh (g) and dry weight (g) measurements. Dry weight (DW) was measured following the drying of fresh biomass at 65 °C for 4 d, and expressed in grams. Dry matter (DM) content was calculated as the ratio of dry weight to fresh weight, multiplied by 100 and presented in percentage.

2.3 Plant Physiological and Photosynthetic Related Parameters

Leaf stomatal conductance measurements were conducted using the Delta-T AP4 porometer (Delta-T Devices-Cambridge, UK) and expressed as mmol H_2O m^{-2} s^{-1}. Relative chlorophyll content values were determined using the SPAD-502 optical chlorophyll meter (Konica Minolta, Osaka, Japan). Leaf chlorophyll fluorescence of PSII (Fv/Fm) was measured with the OptiSci OS-30p Chlorophyll Fluorometer (Opti-Sciences, Hertfordshire, UK).

Fresh plant tissue (six replications/treatment; 0.1 g) was used for chlorophyll extraction. Chlorophyll a (Chl a), chlorophyll b (Chl b), total chlorophyll (total-Chl) and carotenoids (Car) content were calculated (mg g^{-1} fresh weight-FW), by measuring the absorbance at 470, 653 and 666 nm (Multiskan GO, Thermo Fishcer Scientific Oy, Finland) (Richardson et al. 2002; Wellburn 1994).

2.4 Nutrient Content in Leaves and Roots

Following the completion of the experiment, leaf and root tissue samples were collected from each treatment group. Six

replicates were analyzed per treatment, with each replicate consisting of pooled tissue from three plants. Plant tissue was dried to achieve constant weight (at 65 °C for 4 d) and was subsequently burned to ash at 450 °C for 6 h. Following acid digestion (2 M HCl), K and sodium (Na) were determined by flame photometry (Lasany Model 1832, Lasany International, Panchkula, India), whereas P was determined using the molybdate–vanadate method (Chrysargyris et al. 2019). Magnesium (Mg) and calcium (Ca) were determined by an atomic absorption spectrophotometer (PG Instruments AA500FG, Leicestershire, UK). Nitrogen was determined by the Kjeldahl method (BUCHI, Digest automat K-439 and Distillation Kjeldahl K-360, Flawil, Switzerland). Data were expressed in g kg^{-1} of dry weight.

Records of plant water and nutrient solution usage were maintained during the cultivation period. This was conducted by tracking the addition of the modified stock solutions in the NS and water from the replenishment tanks, and then subtracting the nutrients and water that remained in the drainage solutions. Water uptake (mL $plant^{-1}$ day^{-1}) was calculated by recording the total quantity utilized by plants via the replenishment tanks. Water use efficiency (WUE), indicated as the irrigation water productivity, was calculated as the ratio between the biomass produced by a crop and the water consumed, as follows:

$$\mathrm{WUE} = \frac{\text{Biomass (g per plant)}}{\text{Water (L per plant)}} \quad (1)$$

The nutrient use efficiency (NUE) was calculated by considering the input nutrients supplied through the modified stock solutions and the final plant biomass produced. The total NS volume was determined by recording the total volume of the modified stock solutions added to each reservoir (including the initial addition and subsequent applications) and considering the remaining NS at the end of the experiment. Calculations were conducted as follows:

$$\mathrm{NUE} = \frac{\text{Biomass (g per plant)}}{\text{NS (mL per plant)}} \quad (2)$$

2.5 Total Phenolics, Total Flavonoids, Antioxidant Activity, Ascorbic Acid and Total Soluble Sugars

Polyphenols extraction was conducted using six leaf tissue samples (0.7 g) per treatment (two individual plants were pooled/sample) for each treatment. The methanolic extracts were used to determine the total phenolic and flavonoids content. Total phenolic contents were determined using the Folin–Ciocalteu method (at 755 nm) as described previously (Chrysargyris et al. 2020), and were expressed in gallic acid equivalents (mg GAE g^{-1} fresh weight). The total flavonoids were quantified using the aluminium chloride colorimetric method described by Chrysargyris et al. (2016). The absorbance was measured at 510 nm. The total flavonoid content was expressed as rutin equivalents (mg rutin g^{-1} fresh weight).

Antioxidant activity assays were conducted as well, using the 2,2-diphenyl-1-picrylhydrazyl (DPPH), the ferric reducing antioxidant power (FRAP) and the 2,2'-azino-bis(3-ethylbenzothiazoline-6-sulphonic acid (ABTS) methods. Briefly, the DPPH radical scavenging activity of the leaf extracts was measured at 517 nm while the FRAP activity was measured at 593 nm, as described previously (Chrysargyris et al. 2019). The ABTS assay was applied based on the methodology described by Wojdyło et al. (2007). Results were expressed as Trolox ((±)-6-Hydroxy-2,5,7,8-tetramethylchromane-2-carboxylic acid) equivalents (mg trolox g^{-1} of fresh weight).

Ascorbic acid (AA) determination was conducted using the 2,6-Dichloroindophenol titrimetric method as described previously (AOAC 2007). In brief, leaf tissue (0.5 g) was extracted in 10 mL oxalic acid 4.0% and was titrated by the dye solution until the color changed. Data were expressed as mg of AA per 100 gram of fresh weight.

Finally, total soluble solids (TSS) were determined from the juice obtained from plant tissue with a temperature-compensated digital refractometer (model Sper Scientific 300017, Scottsdale, Arizona, USA) at 20 °C, and results were expressed in percentage (%).

2.6 Lipid Peroxidation, Hydrogen Peroxide, and Enzymes Antioxidant Activity

The damage index was assessed by the hydrogen peroxide (H_2O_2) content, and lipid peroxidation by the malondialdehyde (MDA) content. The H_2O_2 was determined by employing the method of Loreto and Velikova (2001). Six leaf tissue samples (two individual plants were pooled/sample) were used for this analysis from each treatment. The H_2O_2 was then measured using 5 to 1000 µM H_2O_2 standards, while the calibration curve was appropriately plotted. Samples and standards were measured at 390 nm, and the results were expressed as µmol H_2O_2 g^{-1} fresh weight. The MDA was determined according to De Azevedo Neto et al. (2006) and the absorbance was recorded at 532 nm and corrected for non-specific absorbance at 600 nm. MDA content was determined using the extinction coefficient of 155 mM cm^{-1}. Results were expressed as nmol of MDA g^{-1} fresh weight.

Antioxidant enzymes activity for superoxide dismutase (SOD) (EC 1.15.1.1) and for catalase (CAT) (EC 1.11.1.6) was assayed as described previously (Chrysargyris et al. 2019). The absorbance was measured at 560 nm for SOD and at 240 nm for CAT. Peroxidase activity (POD) (EC 1.11.1.6) was determined following the increase in absorbance at 430 nm as described previously (Chrysargyris et al. 2020). Results were expressed as enzyme units per mg of protein. The protein content in leaf tissue was measured

Table 1 Effect of nitrogen (N; 100–200 mg L^{-1} as N100, N200) concentration in combination with different levels (decreased 0.66-fold, normal 1-fold, or increased 1.5-fold) of phosphorus (P; 47-70-105 mg L^{-1} as P47, P70, P105) and potassium (K; 250-350-525 mg L^{-1} as K250, K350, K525) in the nutrient solution, on plant height (cm), number of leaves, upper plant (leaves) fresh weight (FW; g), dry weight (DW; g) and dry matter content (DM; %) of sowthistle plants grown in a hydroponic NFT system

N-P-K	Plant height	Number of leaves	Upper plant FW	Upper plant DW	Upper plant DM
T1:N100-P47-K250	26.20 ± 0.67bc	25.75 ± 2.72	26.97 ± 0.99ab	2.44 ± 0.08ab	9.11 ± 0.49
T2:N200-P47-K250	30.30 ± 1.96ab	28.50 ± 3.50	35.37 ± 2.56a	3.02 ± 0.24a	8.55 ± 0.39
T3:N100-P70-K350	23.47 ± 0.78 cd	27.25 ± 2.59	21.55 ± 2.83b	2.60 ± 0.06a	7.83 ± 1.22
T4:N200-P70-K350	21.70 ± 0.58d	24.50 ± 6.06	18.05 ± 3.05b	1.50 ± 0.19b	8.50 ± 0.46
T5:N100-P105-K525	27.98 ± 1.01ab	32.50 ± 7.40	39.42 ± 8.00a	3.14 ± 0.59a	8.05 ± 0.18
T6:N200-P105-K525	31.47 ± 2.37a	23.75 ± 1.25	36.57 ± 3.09a	3.37 ± 0.24a	9.31 ± 0.57

Values represent mean ± SE ($n = 6$). Significant differences ($P < 0.05$) among modified NS are indicated by different letters. Mean values without lettering indicated no significant differences

Table 2 Effect of nitrogen (N; 100–200 mg L^{-1} as N100, N200) concentration in combination with different levels (decreased 0.66-fold, normal 1-fold, or increased 1.5-fold) of phosphorus (P; 47-70-105 mg L^{-1} as P47, P70, P105) and potassium (K; 250-350-525 mg L^{-1} as K250, K350, K525) in the nutrient solution, on leaf stomatal conductance (mmol m^{-2} s^{-1}), SPAD value, chlorophyll fluorescence (Fv/Fm), chlorophylls (a, b, total; mg g^{-1} fresh weight) and carotenoids (mg g^{-1} fresh weight) of sowthistle plants grown in a hydroponic NFT system

N-P-K	Stomatal conductance	SPAD	Chlorophyll fluorescence	Chlorophyll a	Chlorophyll b	Total Chlorophylls	Carotenoids
T1:N100-P47-K250	722 ± 42.5b	38.28 ± 0.63	0.80 ± 0.003	0.90 ± 0.04a	0.34 ± 0.02a	1.25 ± 0.06a	0.17 ± 0.01ab
T2:N200-P47-K250	696 ± 90.5b	35.11 ± 0.94	0.79 ± 0.009	0.73 ± 0.07ab	0.24 ± 0.02b	0.98 ± 0.09bc	0.15 ± 0.02b
T3:N100-P70-K350	588 ± 50.5b	34.41 ± 0.94	0.80 ± 0.005	0.71 ± 0.09b	0.23 ± 0.02b	0.95 ± 0.12c	0.13 ± 0.02b
T4:N200-P70-K350	517 ± 64.1b	35.85 ± 1.34	0.80 ± 0.001	0.92 ± 0.06a	0.35 ± 0.03a	1.27 ± 0.08a	0.18 ± 0.02a
T5:N100-P105-K525	836 ± 30.9b	36.68 ± 1.22	0.81 ± 0.003	0.94 ± 0.04a	0.34 ± 0.03a	1.28 ± 0.07a	0.19 ± 0.004a
T6:N200-P105-K525	1312 ± 277a	35.70 ± 1.94	0.80 ± 0.002	0.92 ± 0.03a	0.29 ± 0.01ab	1.22 ± 0.04ab	0.18 ± 0.001a

Values represent mean ± SE ($n = 6$). Significant differences ($P < 0.05$) among modified NS are indicated by different letters. Mean values without lettering indicated no significant differences

using the Bradford method and bovine serum albumin as a standard.

2.7 Statistical Methods

Analysis of variance (ANOVA) on data was performed by IBM SPSS v.22, and results are presented as treatment mean ± standard error (SE). Duncan's multiple range tests were performed when AVOVA rendered a significant treatment impact at $P < 0.05$.

3 Results

3.1 Drainage Solution pH and Electrical Conductivity Evolution

The evolution of the EC and pH of the drainage solution of each treatment are presented in Figure S1. In general, the EC of the drainage solution of the cultivation of sowthistle plants in the NFT system did not differ among the different NS treatments. During the initial 8-day period the EC fluctuated from 1.5 to 2.0 dS m^{-1}, and after the use of the modified NS, the EC reached the target value of 2.3 dS m^{-1}. The pH values remained at 5.5 to 6.5 during the experiment, while fluctuations occurred among treatments, especially after the 6-day mark (Figure S1).

3.2 Plant Growth

The effects of the different modified NS applications on sowthistle growth-related parameters are presented in Table 1. The application of $NPK_{200-105-525}$ led to increased height of up to 45.0%, while the application of $NPK_{100-47-250}$, $NPK_{100-70-350}$, and $NPK_{200-70-350}$ negatively impacted plant height. In the case of $NPK_{100-70-350}$ and $NPK_{200-70-350}$, this resulted in fresh biomass reduction of up to 54.2%, while $NPK_{200-70-350}$ exhibited decreased dry weight of up to 124.7%. Nevertheless, the number of leaves and the upper plant dry matter content remained unaffected by the examined NSs (Table 1).

3.3 Plant Physiological and Photosynthetic Related Parameters

The effects of the different modified NS applications on sowthistle plant physiology are presented in Table 2. Plants subjected to the $NPK_{200-105-525}$ NS had increased stomatal conductance (up to 153.8%), compared to plants grown with all other NSs. Additionally, the application of $NPK_{100-70-350}$ decreased chlorophyll a content (up to 32.4%), while both

$NPK_{200-47-250}$ and $NPK_{100-70-350}$ treatments produced plants with lower chlorophyll b, total chlorophyll and carotenoids content, exhibiting a decrease of up to 52.2%, 34.7% and 46.1%, respectively (Table 2).

3.4 Nutrient Content in Leaves and Roots

Figure 1 shows the effects of the various modified NS applications on the content of macronutrients in the leaves and roots of sowthistle plants grown in a hydroponic NFT system. The application of $NPK_{100-105-525}$ produced plants with the highest N content, while, interestingly, the application of increased N concentration in combination with the same P and K concentrations ($NPK_{200-105-525}$) produced plants with the lowest N content in leaves (Fig. 1A). The same treatment also produced plants with the lowest K content in leaves, although the opposite was evidenced in roots (Fig. 1B). $NPK_{200-47-250}$ produced plants with the highest leaf P content, noting a 30.7% increase over the lowest leaf P content of plants produced with $NPK_{100-105-525}$. On the contrary, the root P content remained unaffected by the examined parameters (Fig. 1C). The application of $NPK_{200-70-350}$ produced plants with the highest leaf Ca content, exhibiting an overall increase of up to 20.6%, while $NPK_{100-105-525}$ significantly increased root Ca content, compared to $NPK_{100-70-350}$ (Fig. 1D). Magnesium content was the highest with the application of $NPK_{100-70-350}$, in both leaves and roots (Fig. 1E). Furthermore, leaf Na content was

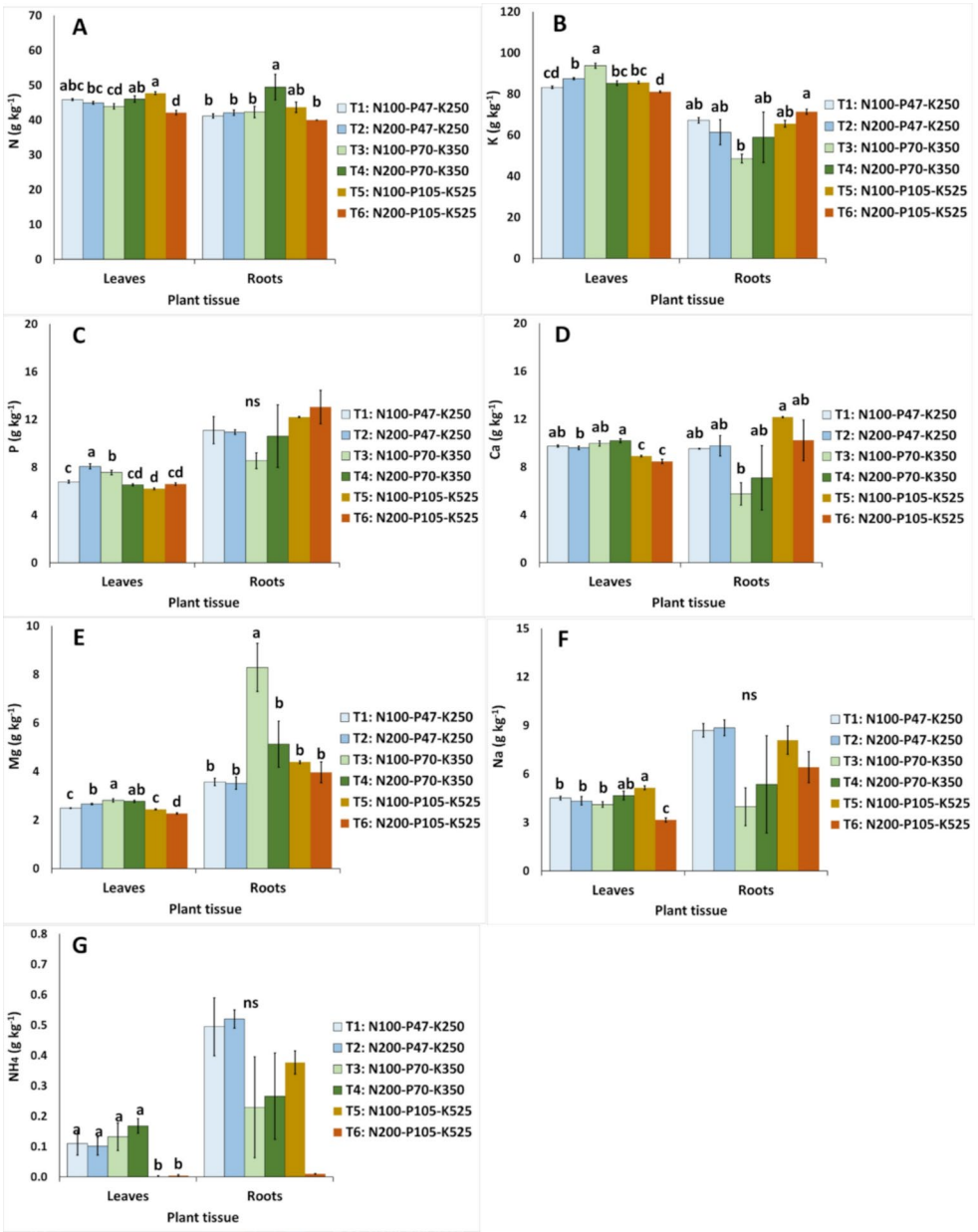


Fig. 1 Effect of nitrogen (N; 100–200 mg L^{-1} as N100, N200) concentration in combination with different levels (decreased 0.66-fold, normal 1-fold, or increased 1.5-fold) of phosphorus (P; 47-70-105 mg L^{-1} as P47, P70, P105) and potassium (K; 250-350-525 mg L^{-1} as K250, K350, K525) in the nutrient solution, on the content of macronutrients in leaves and roots of sowthistle plants grown in a hydroponic NFT system. (**A**) nitrogen-N, (**B**) potassium-K, (**C**) phosphorus-P, (**D**) calcium-Ca, (**E**), magnesium-Mg, (**F**) sodium-Na, and (**G**) ammonium nitrogen-NH_4. Values represent mean ($n=6$). Error bars show SE. On columns, non-significant differences among modified NS are indicated by ns, while significant differences ($P<0.05$) are indicated by different Latin letters according to Duncan's multiple range test

the highest with the application of $NPK_{100-105-525}$, while root Na content remained unaffected (Fig. 1F) and, finally, leaf NH_4 was generally decreased with the application of $NPK_{100-105-525}$ and $NPK_{200-105-525}$, while root NH_4 did not differ between the examined treatment (Fig. 1G).

The use of the modified NS applications did not affect nutrient uptake, water uptake and the nutrient use efficiency of sowthistle plants grown hydroponically. However, the WUE of sowthistle was significantly decreased with the application of $NPK_{200-70-350}$, up to 115.8% compared to the other treatments (Table 3).

3.5 Total Phenolics, Total Flavonoids, Antioxidant Activity, Ascorbic Acid and Total Soluble Sugars

The effects on total phenols content, flavonoids and antioxidant capacity of sowthistle plants are shown in Fig. 2. Total phenolics and total flavonoids content, as well as DPPH of sowthistle were affected by the different modified NS applications. Total phenolics (Fig. 2A) content was increased with the use of $NPK_{100-70-350}$, compared to $NPK_{100-105-525}$, while no differences were found in the remaining treatments. Total flavonoids revealed an increase (up to 74.2%) with the application of $NPK_{100-47-250}$ and $NPK_{100-105-525}$, compared to the rest of the applications (Fig. 1B). Furthermore, the application of $NPK_{200-105-525}$ generally decreased DPPH up to 40.8% (Fig. 2C). The different NS applications did not affect FRAP (Fig. 2D) and ABTS (Fig. 2E), with mean values to be 0.72 and 0.34 mg trolox g^{-1} of Fw for FRAP and ABTS, respectively.

Considering the effects on total soluble sugars and ascorbic acid of sowthistle plants (Fig. 3), elevated TSS values (up to 266.7%) were observed with the use of $NPK_{200-70-350}$ compared to the other applications (Fig. 3A). Furthermore, the AA content was significantly increased with the application of $NPK_{100-105-525}$, while, interestingly, the increase of N ($NPK_{200-105-525}$) produced plants with the lowest AA content (Fig. 3B).

Table 3 Effect of nitrogen (N; 100–200 mg L^{-1} as N100, N200) concentration in combination with different levels (decreased 0.66-fold, normal 1-fold, or increased 1.5-fold) of phosphorus (P; 47-70-105 mg L^{-1} as P47, P70, P105) and potassium (K; 250-350-525 mg L^{-1} as K250, K350, K525) in the nutrient solution, in the nutrient solution on the nutrients and water uptake, nutrient use efficiency (NUE) and water use efficiency (WUE) of sowthistle plants grown in a hydroponic NFT system

*N-P-*K	Nutrients uptake (mL $plant^{-1}$)	Water uptake (L $plant^{-1}$)	NUE (g DW mL^{-1} NS)	WUE (g DW L^{-1} H_2O)
T1:N100-P47-K250	15.95 ± 1.66	3.64 ± 0.25	0.17 ± 0.00	0.67 ± 0.04a
T2:N200-P47-K250	14.19 ± 0.09	4.11 ± 0.38	0.21 ± 0.00	0.74 ± 0.07a
T3:N100-P70-K350	14.29 ± 0.00	3.39 ± 0.41	0.18 ± 0.00	0.77 ± 0.09a
T4:N200-P70-K350	14.29 ± 0.00	3.94 ± 0.49	0.11 ± 0.00	0.38 ± 0.05b
T5:N100-P105-K525	14.29 ± 0.00	3.87 ± 0.21	0.22 ± 0.00	0.81 ± 0.04a
T6:N200-P105-K525	14.29 ± 0.00	4.10 ± 0.06	0.23 ± 0.00	0.82 ± 0.01a

Values represent mean ± SE ($n = 3$). Significant differences ($P < 0.05$) among modified NS are indicated by different letters. Mean values without lettering indicated no significant differences. DW: indicates dry weight

3.6 Lipid Peroxidation, Hydrogen Peroxide, and Enzymes Antioxidant Activity

The effects on hydrogen peroxide, lipid peroxidation indicated by the MDA content, and antioxidant enzymes activity (SOD, CAT, and POD) of sowthistle plants are presented in Fig. 4. The different applications significantly affected the stress response of sowthistle plants. The hydrogen peroxide levels increased (up to 58.7%) in plants grown in $NPK_{200-70-350}$, compared to all the other treatments (Fig. 4A). MDA increased (up to 36.1%) with the application of $NPK_{200-47-250}$, while the application of $NPK_{100-70-350}$, $NPK_{100-105-525}$, and $NPK_{200-105-525}$, produced plants with the lowest MDA content (Fig. 4B). SOD activity increased in plants with $NPK_{200-47-250}$, $NPK_{100-105-525}$, and $NPK_{200-105-525}$, compared to the $NPK_{100-70-350}$ and $NPK_{200-70-350}$ (Fig. 4C). A similar pattern was observed for both CAT (Fig. 4D) and POD (Fig. 4E) activities. Therefore, CAT activity was increased with the application of $NPK_{100-105-525}$, compared to all treatment except the $NPK_{200-70-350}$ treatment. In case of POD, increased activity (up to 39.6%) was found in plants growing in $NPK_{100-105-525}$, compared to all other treatments.

4 Discussion

The current examination was conducted to evaluate the response of sowthistle to different N, P, and K rates in hydroponics, specifically evaluating responses related to plant growth, productivity, physiology, stress response and nutrient status. Previous investigations in soilless cultures revealed that the total level of N supply had a substantial impact on the yield and metabolic functions of WEPs (Chrysargyris et al. 2024; Papadimitriou et al. 2024), including common sowthistle (Chrysargyris and Tzortzakis 2023). The latter study revealed that sowthistle responded well to N concentrations of 100 and 200 mg L^{-1} in the NS in terms of plant growth, total phenolics production and antioxidant activity, whereas the higher N concentration was suggested due to the increased flavonoids content and irrigation

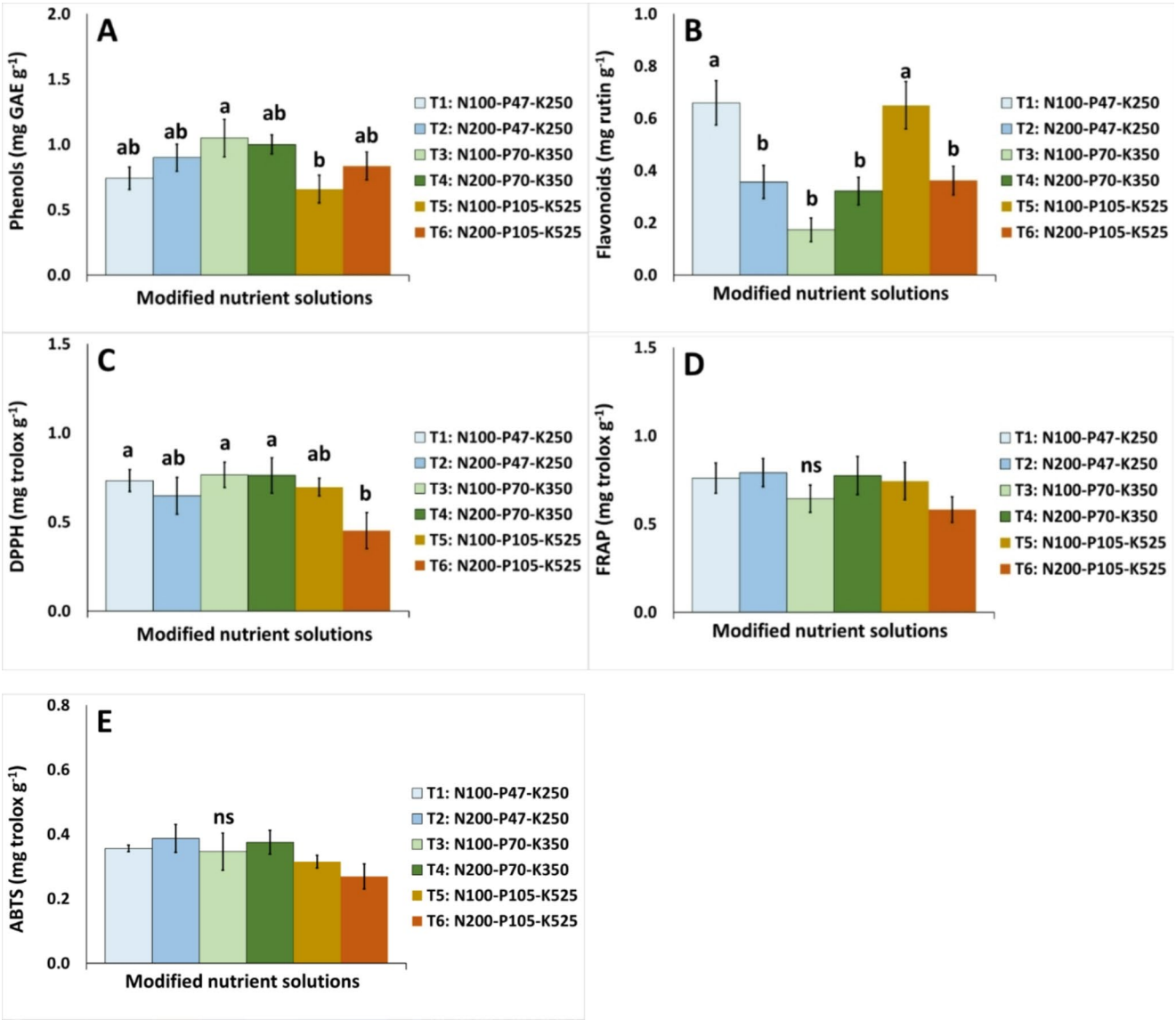


Fig. 2 Effect of nitrogen (N; 100–200 mg L^{-1} as N100, N200) concentration in combination with different levels (decreased 0.66-fold, normal 1-fold, or increased 1.5-fold) of phosphorus (P; 47-70-105 mg L^{-1} as P47, P70, P105) and potassium (K; 250-350-525 mg L^{-1} as K250, K350, K525) in the nutrient solution, on (**A**) total phenols (mg GAE g^{-1} fresh weight), (**B**) flavonoids (mg Rutin g^{-1} fresh weight), antioxidant activity – (**B**) DPPH, (**C**) FRAP, (**D**) ABTS (mg Trolox g^{-1} fresh weight) of sowthistle plants grown in a hydroponic NFT system. Values represent mean ($n=6$). Error bars show SE. On columns, non-significant differences among modified NS are indicated by ns, while significant differences ($P<0.05$) are indicated by different Latin letters according to Duncan's multiple range test

water productivity. However, the study of Chrysargyris and Tzortzakis (2023), used 350 mg K L^{-1} and 70 mg P L^{-1} in the NS, based on previous studies on wild species hydroponic cultivation. These values, however, may not be the most ideal ones for the cultivation of sowthistle plants. Thus, the current study adopted two N concentrations (100 and 200 mg L^{-1}) as the basis for the examined NS applications, whereas three P and K levels (decreased 0.66-fold, normal 1-fold, or increased 1.5-fold) were also examined, to evaluate the interplay between these three important macronutrients, as their availability affects the growth and development of plants (Deng and Li 2022).

Sowthistle plants grown in pots using a soil, sand, and vermiculite mixture (1/1/1; *w/w/w*) exhibited enhanced plant growth as N rates in the N-P-K fertilization application increased (from 100 to 600 mg L^{-1}). However, changes to P and K levels did not have a significant effect on yields, underscoring the prominent role of N in promoting sowthistle plant growth and yield (Carrascosa et al. 2022). Similarly, Chrysargyris and Tzortzakis (2023) observed that, in soilless cultivation, sowthistle fresh and dry biomass was

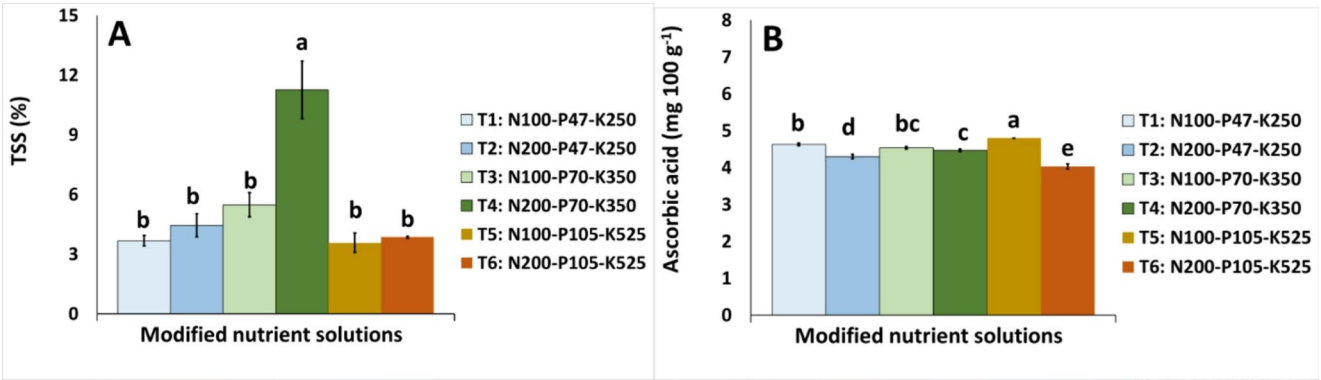


Fig. 3 Effect of nitrogen (N; 100–200 mg L^{-1} as N100, N200) concentration in combination with different levels (decreased 0.66-fold, normal 1-fold, or increased 1.5-fold) of phosphorus (P; 47-70-105 mg L^{-1} as P47, P70, P105) and potassium (K; 250-350-525 mg L^{-1} as K250, K350, K525) in the nutrient solution, on (**A**) total soluble sugars (TSS: %) and (**B**) ascorbic acid (AA) (mg 100 g^{-1} fresh weight) of sowthistle plants grown in a hydroponic NFT system. Values represent mean ($n = 6$). Error bars show SE. On columns, significant differences ($P < 0.05$) are indicated by different Latin letters according to Duncan's multiple range test

increased when grown at ≥100 mg L^{-1} N in the NS. However, no significant differences in plant height, and fresh and dry biomass were observed among the applications of 100, 200 and 300 mg N L^{-1}. These differences among the above-mentioned studies may be attributed to the differences in the experimental design, the cultivation methods applied (i.e. hydroponic, potted soil) and the duration of the cultivation period. Similarly, in the current study, the increased rate of N (200 mg L^{-1}) generally led to an increase in plant height, above-ground FW and DW, under decreased (0.66-fold) and increased (1.5-fold) P and K levels. However, the application of 1-fold levels of P and K in the NS generally negatively affected plant growth parameters, especially with the increased N rate (200 mg L^{-1}). Lasheen et al. (2021) observed differences regarding toothbrush tree (*Salvadora persica* L.) growth, depending on the NPK rates, while increased rates N, P and K resulted in greater biomass production, as per the current study. In addition, Sapkota et al. (2019) reported that different lettuce (*Lactuca sativa* L.) cultivars (Buttercrunch and Black Seeded Simpson) biomass production was modulated by the different N, K and Ca rates of the hydroponic NS, with excess or deficient levels negatively affecting growth. However, the short period of sowthistle cultivation may not have produced significant reductions in growth and yield. These discrepancies could be attributed to various factors, including plant species and their sensitivity to ionic proportions (Fallovo et al. 2009). Ultimately, both $NPK_{100-105-525}$ and $NPK_{200-105-525}$ resulted in increased plant height and biomass production, suggesting a positive correlation between higher levels of P and K, and sowthistle plant growth. Yan et al. (2015) observed that by increasing the P concentration in the NS up to 0.64 mM enhanced the growth of *Zizania latifolia* (Griseb.) Stapf cultivated hydroponically. This is because P availability significantly affects many physiological and metabolic processes, including biomass production. Similarly, K influences processes such as ion homeostasis, stomatal conductance and photosynthesis, all of which affect plant growth and development. In addition, previous research has confirmed the synergistic interaction between K and P in promoting plant growth (Naciri et al. 2022).

Nitrogen is required by plants as a component of cellular biomolecules, including proteins, chlorophylls and plant growth regulators. Balanced N nutrition is vital for crops, while deficiency affects photosynthesis, and chlorophyll contents (Sinha and Tandon 2020). Similarly, P deficiency symptoms include the disruption of CO_2 assimilation, by hindering the transport of fixed carbon from chloroplast to the cytosol, thus reducing the photosynthetic capacity of plants (Loudari et al. 2022). In addition, a positive correlation between the photosynthetic rate of plants and the contents of NH_4^+ and K^+, exhibiting a strong synergistic relationship. Furthermore, the optimization of N and K applications could aid in optimizing leaf N allocation and photosynthetic N use efficiency. Thus, limited N, P and K has pronounced effects on the physiology of plants, including cell division, expansion and permeability, as well as photosynthesis (Hossain et al. 2010). However, increased N rates could interfere negatively on photosynthesis. Bernardi et al. (2015) observed, increased N levels negatively affected parameters such as photosynthesis, while intermediate K levels had a positive effect on *Citrus sinensis* plants. Nevertheless, P did not exert great influence on photosynthesis. In addition, decreased N, P, and K fertilization rates from the optimum resulted in decreased chlorophyll contents in rice (*Oryza sativa* L.). In the current study, the chlorophyll content (Chl a, Chl b, total Chl) was negatively influenced by $NPK_{200-47-250}$ and $NPK_{100-70-350}$ applications, ascribed by the respective increase of N application with decreased P and K levels, and the decrease of N application with intermediate P and K

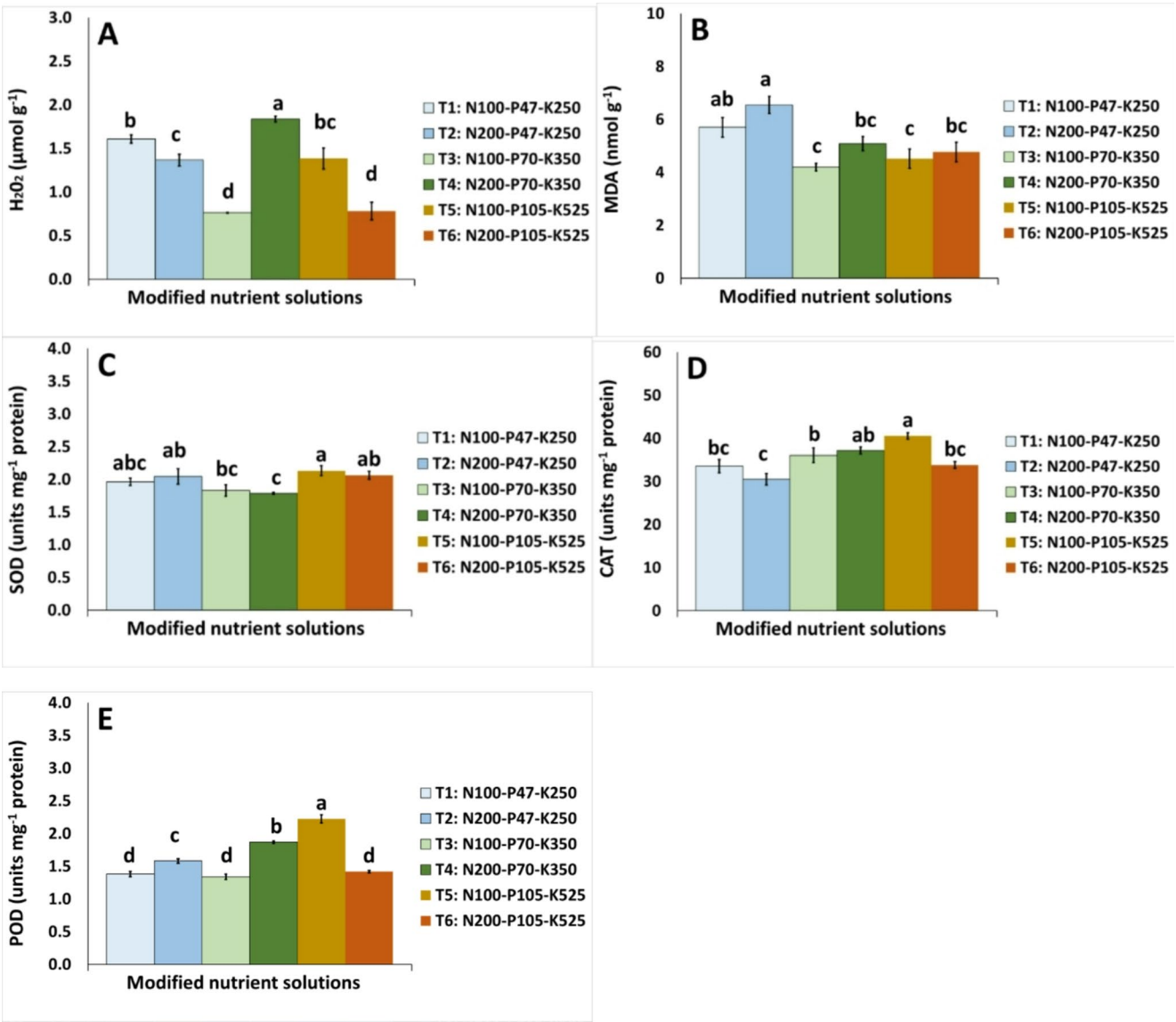


Fig. 4 Effect of nitrogen (N; 100–200 mg L^{-1} as N100, N200) concentration in combination with different levels (decreased 0.66-fold, normal 1-fold, or increased 1.5-fold) of phosphorus (P; 47-70-105 mg L^{-1} as P47, P70, P105) and potassium (K; 250-350-525 mg L^{-1} as K250, K350, K525) in the nutrient solution, on (**A**) hydrogen peroxide - H_2O_2 (µmol g^{-1}), (**B**) lipid peroxidation - MDA (nmol g^{-1}) and antioxidant enzymes activity of (**C**) superoxide dismutase (SOD; units mg^{-1} protein), (**D**) catalase (CAT; units mg^{-1} protein), and (**E**) peroxidase (POD; units mg^{-1} protein) of sowthistle plants grown in a hydroponic NFT system. Values represent mean ($n=6$). Error bars show SE. On columns, significant differences ($P<0.05$) are indicated by different Latin letters according to Duncan's multiple range test

levels. The variations in leaf chlorophyll content observed under different NPK applications rates may be attributed to imbalances in nutrient concentrations, as suggested by Hossain et al. (2010). Additionally, large variations in the N: K ratio may affect leaf chlorophylls and chlorosis; increased ratios may accelerate chlorophyll decomposition, while synchronous increases in N and K supplementation, ensuring an appropriate leaf N: K ratio (Li et al. 2022a). Finally, the increased stomatal conductance observed in the application of $NPK_{200-105-525}$. Similarly, Bernardi et al. (2015) and Khan et al. (2023) found a positive correlation between stomatal conductance and increased K and P rates, highlighting the importance of K and P in regulating stomatal function. Finally, both N and K contribute to maintaining cell osmotic pressure (Li et al. 2022a).

Nitrogen and P nutrition are closely related, as they are characterized by a mutual interaction in their uptake and assimilation (Kumar et al. 2021). In general, increased rates of P regulate the uptake of N, under decreased N availability (Schleuss et al. 2020). The current study, which observed increased N contents of sowthistle plants with the application of increased (1.5-fold) rates of P and K, under the

lower N concentration of the NS (100 mg L^{-1}), supports these findings. El-Sherbeny et al. (2015) reported significant increases in the N content of purslane (*Portulaca oleracea* L.) with increased K fertilization rates. However, Jiang et al. (2023) saw increased N content under P deficient NS in the sand cultivation of strawberry (*Fragaria ×ananassa* Duch.). The researchers also reported a significant increase of the plant P content (close to the control application NS), on the soilless cultivation (sand culture) of under N deficient NS. In contrast, the current study observed increased P content of leaves with the highest N rates in conjunction with decreased (0.66-fold) rates of P, while increases in the rates of both P and K resulted in decreased sowthistle P contents. However, Lasheen et al. (2021) observed that, by modifying the rates of N, P and K in the fertilization of *S. persica* L. plants, the P content of leaves did not differ significantly among treatments. These may be attributed to the differences among the examined species, the duration of the cultivation period, as well as the growth rate of plants. Regarding K, its uptake by plants is primarily influenced by the application of N and K, while P has a less significant impact (Arbačauskas et al. 2023). An insufficient application of N impacts K uptake, leaf K contents are positively affected by using NS with a high proportion of K (Fallovo et al. 2009). This was not evidenced in the current study, as the $NPK_{100-70-350}$ NS resulted in the greatest accumulation of K in sowthistle plant tissues. In addition, K availability significantly influences the uptake and accumulation of Ca and Mg (Li et al. 2019). This was evident in the current study too, as increased K concentrations in the NS led to a general decrease in the content of Ca and Mg in sowthistle plants. Elevated K concentrations in the NS may also hinder the absorption of NH_4 by plants, resulting in decreased contents of NH_4 in leaves. This is attributed to the competition between ions, especially to the monovalent ones, for uptake mechanisms within the plant (Li et al. 2023). The current study supports this, demonstrating that the 1.5-fold levels of K resulted in a significant decrease in NH_4 accumulation, regardless of N concentrations in the NS. In addition, the application of $NPK_{200-70-350}$ resulted in a reduction in WUE. This indicates that the utilization of a lower N application rate, in combination with standard P and K rates could be a more sustainable approach, as it minimizes fertilizer usage. Conversely, NUE remained unaffected by the examined parameters, aligning with the findings of Chrysargyris et al. (2024) on hydroponic purslane (*P. oleracea* L.) cultivation.

Soilless cultivation of WEPs may ensure a stable supply of high-quality plant material, demonstrating enhanced secondary metabolite production in various species compared to both wild and soil-grown plants. This may be attributed to various factors, including optimized nutrient delivery (Atherton and Li 2023). This study, along with a limited number of previous investigations (Chrysargyris and Tzortzakis 2023; Gkotzamani et al. 2024), has demonstrated the potential for commercial exploitation of sowthistle with the use of soilless cultivation systems to produce high-quality plant material. Notably, several indices, including total phenolics content and flavonoids, exhibited equivalent of increased values in the current study, compared to those observed in wild sowthistle populations (Nouidha et al. 2023). In terms of fertilization applications, N-limitation may increase the biosynthesis of flavonoids (Ibrahim et al. 2012). In fact, the lower N rate (100 mg L^{-1}) led to the increase of flavonoids content in sowthistle plants, under decreased (0.66-fold) or increased (1.5-fold) levels of P and K. This is coupled with the positive impact of increased K and P fertilization on flavonoids. However, in pak choy (*Brassica rapa* subsp. *chinensis* [L.] Hanelt), short-term P omission may promote flavonoid accumulation (Waqas et al. 2023). Cultivated WEPs demonstrate diverse responses in terms of oxidative stress and lipid peroxidation, as well as antioxidant enzyme activities, observed based on fertilization regimes (Chrysargyris and Tzortzakis 2023; Villani et al. 2023). This occurs as nutrient deficiency disrupts the balance between the production of reactive oxygen species (ROS) and antioxidant defense mechanisms (Du et al. 2019). In fact, N was found to have a profound effect on hydrogen peroxide production, and on the induction of antioxidant enzymes such as SOD and CAT of sowthistle plants cultivated hydroponically (Chrysargyris and Tzortzakis 2023). This occurs as N limitation affects electron transport systems, photosynthesis, and senescence (Tewari et al. 2007). Notably, P-deficiency may also lead to the production of ROS, as it affects the photosynthetic CO_2 fixation and photosynthetic electron transport (Lin et al. 2012). In addition, K-deficiency impacts electron transport carriers, leading to the accumulation or reducing power (NADPH) and the generation of ROS (Tewari et al. 2007). The current study observed a reduction in the H_2O_2 content, with the increased N rate (200 mg L^{-1}), at decreased (0.66-fold) and increased (1.5-fold) levels of P and K. This finding aligns with the observations of Chrysargyris and Tzortzakis (2023), who reported increased H_2O_2 with the application of 100 mg N L^{-1} compared to 200 mg N L^{-1} in the NS of hydroponically cultivated sowthistle. However, the inverse occurred under normal (1-fold) levels of P and K, highlighting the importance of balanced N, P, and K levels. The capacity of the antioxidant systems contribute greatly to this process, comprising of multiple enzymes to reduce the harmful effects of ROS (Li et al. 2016). Particularly, the increased H_2O_2 observed with the application of $NPK_{200-70-350}$ was accompanied by decreased SOD levels, whereas increased SOD in the rest of the treatments, excluding $NPK_{100-47-250}$

and $NPK_{100-70-350}$, suggest that SOD is actively managing the accumulation of H_2O_2 under these conditions. Furthermore, an increase in CAT and POD was observed with the application of $NPK_{100-105-525}$, accompanied by decreased H_2O_2 and MDA levels, indicating that plants were undergoing adaptive responses to combat the production of ROS (Chrysargyris et al. 2024). In addition, sowthistle plants that were supplied with $NPK_{200-70-350}$ exhibited increased TSS compared to the rest of the treatments. Increased TSS levels under elevated N and K fertilization can be attributed to their influence in key physiological and metabolic processes. Specifically, N supply has a significant effect on photosynthesis and carbohydrate production, while K contributes to photosynthetic carbon assimilation and the carbohydrate metabolism, thus influencing TSS accumulation (Li et al. 2022b; Marschner 2011). The study of Braun et al. (2016) showed that decreasing N fertilization negatively influenced TSS accumulation in potato (*Solanum tuberosum* L.) leaves, while Kumari et al. (2021) reported that increased N rates enhanced TSS in stevia (*Stevia rebaudiana* [Bertoni]). However, Chrysargyris and Tzortzakis (2023) reported that excessive N fertilization may have a depressive effect on TSS of sowthistle leaves, highlighting the importance of balanced fertilization. Finaly, similar to this study, research on sowthistle has indicated that increased fertilization may lead to decreases in the AA content (Hajisolomou et al. 2024), while increased N application negatively affected the AA content in horticultural crops cultivated hydroponically (Mahlangu et al. 2016).

5 Conclusions

The results of the current study highlight the commercial exploitation potential of sowthistle as an underutilized wild edible plant, through the use soilless cultivation methods. Nitrogen, phosphorus and potassium fertilization have a significant role in enhancing plant growth, yield and quality, and their relative rates affected plant metabolism. This research provided an insight into the application rates of these macronutrients in a hydroponic nutrient solution for the successful cultivation of sowthistle. In general, decreased (0.66-fold) and increased (1.5-fold) phosphorus and potassium levels stimulated plant growth, chlorophylls, carotenoids and flavonoids, while the decreased nitrogen levels (100 mg L^{-1}) stimulated ascorbic acid content, resulting in higher nutritive value edible products. The application of increased phosphorus and potassium levels suppressed lipid peroxidation and oxidative damage which was mirrored to the decreased total phenolics and antioxidant capacity. The role of phosphorus was fundamental to the appropriate nitrogen uptake in plants, as the increased rates of phosphorus regulated the nitrogen uptake, under decreased nitrogen availability. Similarly, the greatest accumulation of potassium in sowthistle was found under the decreased nitrogen levels (100 mg L^{-1}) and 1-fold phosphorus and potassium. As hypothesized, the rates of phosphorus and potassium can adjust any possible nitrogen shortage in the nutrient solution affecting plant growth and metabolism. Our findings indicate that adjusting phosphorus and potassium levels, either by increasing or decreasing them, can stimulate the growth and quality of cultivated sowthistle. However, to further optimize sowthistle production in soilless cultivation, future research should explore the impact of various aspects of the nutrient solution, including the balance between macrocations (potassium: calcium: magnesium) as well as the impact of micronutrients in the nutrient solution or via foliar application. Additionally, applying controlled stress (eustress) may provide valuable insights into enhancing organoleptic properties, nutritional value and bioactive components of sowthistle.

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Declarations

Conflict of interest The authors declare no conflicts of interest.

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