

Research Article

Effects of NaCl concentrations on glucosinolate and carotenoid biosynthesis in Chinese cabbage sprouts grown under light and dark conditions

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Abstract

This study aimed to determine the effect of NaCl concentration (0, 50, 100, 150 and 200 mM) on glucosinolate and carotenoid biosynthesis in Chinese cabbage (*Brassica rapa* ssp. *pekinensis*) sprouts under light and dark conditions. In terms of light, the total glucosinolate content significantly decreased from all NaCl concentrations compared to the control, while the carotenoid content sharply decreased in a progressive manner throughout the entire NaCl gradient, mostly due to β -carotene and lutein. The total glucosinolate content under dark conditions initially reduced at 50-150 mM but at 200 mM almost reached 74% of the control level, whereas the total carotenoid content exhibited a clear biphasic response, increasing slightly at 50 mM and then decreasing as NaCl increased. When the individual compounds were analysed, it was found that the profile of glucosinolates was not consistently affected by NaCl; aliphatic glucosinolates (such as glucoraphanin and neoglucobrassicin) tended to decrease with increasing salinity, whereas indolic glucosinolates (glucobrassicin and 4-hydroxyglucobrassicin) generally increased with increasing salinity in both light and dark conditions. These results indicate that light condition affects both direction and magnitude of NaCl effects on secondary metabolism, such as recovery of Chinese cabbage sprout (CAB) in response to high salinity, while light-grown CAB shows a dose-independent, sustained repression of secondary metabolism after a low-salt threshold. This study serves as a foundation for developing optimized elicitation strategies with NaCl to improve the nutraceutical quality of Chinese cabbage sprout in functional food.

Keywords: NaCl, Biosynthesis, Glucosinolate, Carotenoid, Light and Dark, Chinese Cabbage

Introduction

Chinese cabbage (*Brassica rapa* ssp. *pekinensis*) is one of the most widely cultivated leafy vegetables in East Asia and is increasingly consumed worldwide as young sprouts and microgreens, which are prized for their short production cycle, high density of bioactive phytochemicals, and convenience for indoor or vertical farming systems. Among the phytochemicals that determine the nutritional and functional quality of Brassica sprouts, glucosinolates (GSLs) and carotenoids are of particular interest because of their well-documented roles in human health and in the plant's own defense and photoprotective systems (Maselesele *et al.*, 2022).

Glucosinolates are sulfur- and nitrogen-containing secondary metabolites found almost exclusively in the order Brassicales, where they are classified as aliphatic, indolic, or aromatic according to their amino acid precursors (Zhao *et al.*, 2026). Upon tissue disruption, GSLs are hydrolyzed by the enzyme myrosinase into isothiocyanates and other bioactive breakdown products that contribute to the pungent flavor of Brassica vegetables and have attracted considerable attention for their antioxidant, anti-inflammatory, and

cancer-chemopreventive properties in humans (Baldelli *et al.*, 2025). Carotenoids, in contrast, are isoprenoid pigments synthesized via the plastidial methylerythritol phosphate (MEP) pathway; they are essential components of the photosynthetic apparatus, where they participate in light harvesting and in the dissipation of excess excitation energy, and their dietary intake is linked to provitamin A activity and reduced risk of several chronic diseases (Swapnil *et al.*, 2021). Given that both metabolite classes are able to be accumulated as a response to environmental cues, it is a practical solution that the nutraceutical value of Brassica sprouts can be enhanced without genetic modification through the manipulation of pre-harvest growing conditions. It was also reported that glucosinolates and their derivatives in sprouts and microgreens varied during their cultivation and postharvest handling (Michalczyk, 2025).

Light is one of the most important environmental factors that regulate secondary metabolism in sprouts and microgreens. Light-induced transcription activation of carotenoid biosynthesis genes (PSY, PDS, β OHASE1) and their association with light regulators like HY5 corresponds well with the dependence of carotenoid accumulation on light conditions, with significantly higher levels in light-

grown vs. etiolated/dark-grown tissue (Kim & Eom, 2025). The direct evidence of this pattern has been demonstrated in several Brassica species, such as Chinese cabbage (*B. rapa* ssp. *pekinensis*), pak choi, cauliflower, kale and turnip cabbage grown under different LED spectra (Jeong *et al.*, 2019) and showed different response in terms of different light conditions and time of sprouting on harmful and beneficial aspects of rutabaga sprouts in comparison to their roots and seeds (Paško *et al.*, 2019). The quality and duration of light also influence GSL metabolism; red and blue light promoted the biosynthesis of glucosinolates and phenolics in radish and mustard sprouts, and longer daily light period resulted in higher levels of glucosinolates in Chinese kale sprouts than exposure to continuous darkness (Wang *et al.*, 2021). In contrast, dark-grown (etiolated) sprouts often exhibit reduced carotenogenesis and modified GSL amounts, as a strong association between the photomorphogenesis and the production of secondary metabolites in seedlings of Brassicaceae is found.

The effects of salinity on secondary metabolism in Brassica crops are concentration-dependent and more complex than light, being a further environmental factor that can influence secondary metabolism. NaCl is an abiotic stressor which can increase primary metabolism related to defense under mild salt stress, but severe salt stress can cause growth inhibition and decrease in pigment production due to osmotic and ionic stress. Concentrations of total glucosinolates of broccoli sprouts were reduced with low to moderate concentrations of NaCl, but specific indolic glucosinolates and the cancer-protective compound sulforaphane were selectively increased, suggesting a change in glucosinolate composition and not a general effect (Lam *et al.*, 2024). In Brassica rapa seedlings, chloride salinity had a similar effect on aliphatic glucosinolates in the shoot, which was accompanied by the down-regulation of key biosynthetic genes, while sulfate salts induced an up-regulation of the same genes, leading to an increase in indolic and aromatic glucosinolates (Aghajanzadeh *et al.*, 2018). Higher concentrations of NaCl (40 mM to 100 mM) have also been reported to decrease aliphatic and indolic glucosinolate concentrations in broccoli florets, and the effect of combined NaCl and light-quality treatments in mustard showed that NaCl led to decreased concentrations of chlorophyll and glucosinolates while promoting biomass accumulation; however, the effect of red light was to increase the concentrations of both the pigments and glucosinolates (Sarikamis & Çakir, 2017). In conclusion, the results presented here suggest that salt and light may affect secondary metabolite production in Brassica sprouts in opposite directions, and that their effects may be synergistic, depending on species, tissue and salt concentration.

Although this is emerging, the majority of the studies have focused on either salinity or light alone, and few on the interaction between these two factors within the context of glucosinolate and carotenoid biosynthesis of Chinese cabbage (*B. rapa* ssp. *pekinensis*) sprouts, which are an economically important vegetable crop and a popular food source of functional sprouts in East Asia. NaCl concentration

under light and dark conditions needs to be systematically evaluated since both light and salinity have been shown to independently induce/reduce similar pathways of secondary metabolism that are of interest to sprout producers who are constantly searching for low-cost approaches, not genetic, to improve nutraceutical content (e.g. salt priming and light management). Therefore, the present study investigated the effects of a range of NaCl concentrations on glucosinolate and carotenoid accumulation in Chinese cabbage sprouts grown under light and dark conditions, with the aim of identifying growing conditions that optimize the nutritional and functional quality of this widely consumed sprout crop (Samuolienė *et al.*, 2026).

Materials and methods

Plant materials and growth conditions

Seeds of Chinese cabbage (*Brassica rapa* ssp. *pekinensis*) were purchased from Asia Seed Co., Ltd (Seoul, Korea). The seed (100 seeds per plastic pot 11 × 11 cm) was sown in plastic pot and was grown in plant growth chamber at 25 °C under white light of 16 h day/8 h night and 24 h dark photocycle for 7 days. Chinese cabbage sprouts were first grown in light (16 h light/8 h dark) or dark (24 h dark) for 7 days to study the combined effect of light and NaCl treatment on the biosynthesis of glucosinolates and carotenoids. The seedlings were then subjected to 0, 50, 100, 150 or 200 mM NaCl for another 7 days, under the same light or dark conditions as before. For biological repeats, 3 plastic pot was used for each individual and a number of seedlings was harvested from each sample in plastic pot in the growth chamber. All the samples were frozen in liquid nitrogen upon collection and stored at -80 °C until use. Glucosinolate and carotenoid analysis was performed on sprouts.

The extraction of glucosinolates and HPLC analysis

Cabbage powder was prepared by freeze-drying and extracted using previously reported procedures with slight modification (Kim *et al.*, 2013) 100 mg of the freeze-dried cabbage powder was extracted with 1.5 mL of 70% (v/v) boiling aqueous methanol at 70 °C for 5 min in water-bath followed by centrifugation at 4 °C for 10 min at 12,000 rpm. The supernatant was collected into a 15 mL conical tube (H20015; Hyundai Micro Co., Ltd. Seoul, Korea) and the resultant pellets were re-extracting a further two times using the same procedure. The same procedure was repeated with the collected supernatants as with the crude glucosinolate extracts, except that the mini-column was flushed with 3ml of distilled water. Next, 75 µL of purified arylsulfatase was added to the eluate and incubated at room temperature overnight to desulfate it. Afterwards, the samples of desulfated glucosinolate were washed through three times with 0.5 mL of ultrapure water in a 2.0 mL safe-lock microcentrifuge tube (Eppendorf, Seoul, Korea) and filtered through 0.22 µm PTFE syringe filters (Sterlitech Corp., USA) into a brown vial. Glucosinolate contents were separated using an Agilent Technologies 1200 series HPLC system (Palo Alto, CA, USA) with

an Inertsil® ODS-3 column (150 × 3.0 mm i.d., particle size 3 µm; GL Sciences, Tokyo, Japan) and an Inertsil® ODS-2 guard column (10 × 2.0 mm i.d., particle size 5 µm; GL Sciences). HPLC conditions were as follows: detection wavelength – 227 nm, flow rate – 0.2 mL/min, oven temperature – 40 °C, injection volume – 20 µL. The gradient program used was as follows: Solvent A, HPLC grade water; Solvent B, HPLC grade acetonitrile; 0-18 min, 7%-24% B; 18-32 min, 24% B; 32.01 min, rapid drop to 7% B; and 32.01-40 min, 7% B (total 40 min). The HPLC retention times, the HPLC areas and the response factors of each glucosinolate were compared to those of the external standard, sinigrin (0.5 mg/5 mL) (ISO 9167-1, 1992) to identify and quantify each glucosinolate.

Extraction of carotenoids and HPLC analysis

Sample preparation and HPLC analyses of carotenoids followed previously described procedures (Tuan *et al.*, 2012). In both rectangular and oval Chinese cabbage 15 mL conical tubes 3 mL of ascorbic acid/ethanol (0.1%, w/v) was added on powders. The mixture was strongly vortex for 20 s and then incubated in a water bath set at 85 °C for 5 min. Saponification was then performed by the addition of 120 µL of potassium hydroxide (80%, w/v) to remove any potentially interfering oils. Each tube was then incubated at 85 °C for 10 min followed by 5 min on ice to halt the reaction and 50 µL of an internal standard (25 ppm of β-apo-8'-carotenal) was then added to the samples. Then 1.5 mL of cold distilled water and 1.5 mL of hexane (SAMCHUN Chemical, Pyeongtaek, Korea) were added to the sample and the mixtures were centrifuged at 4°C at 1,200 rpm to obtain the supernatants from the layers. The extraction procedure was repeated twice for a total of three extractions. The collected aliquots were then dried in a fume hood under nitrogen gas at room temperature and the dried samples were then resuspended in 300 µL of dichloromethane/methanol (50:50 v/v). The final extracts were placed in brown-coloured vials after being filtered through 0.45 µm PTFE syringe filters. The carotenoid contents of each sample were separated using a C30 YMC column (250 × 4.6 mm, 3 µm; Waters Corporation, Milford, MA, USA) in an Agilent Technologies 1100 series liquid chromatograph (Palo Alto, CA, USA) fitted with a photodiode array detector, at 450 nm. The conditions for HPLC analysis were set as follows: injection volume, 20 µL and flow rate, 1.0 mL/min. The mobile phase consisted of a binary mixture of Solvent A: Methanol: Water (92:8 v/v) with 10 mM ammonium acetate and Solvent B: Methyl tert-butyl ether (100%). The individual carotenoids were identified by comparing the retention times and by spiking and quantified by referring to the appropriate calibration curve.

Statistical analysis

All the growth parameter values are stated as the mean±SD of five samples. All values of the content of phenylpropanoids in the Tartary buckwheat sprouts are presented as mean±SD of three samples. Data collection for growth and phenylpropanoid were analysed statistically by using Statistical Analysis System software (SAS, system

9.4, 2013, SAS Institute Inc., Cary, NC, USA). Duncan's multiple range test (DMRT) at 0.05 level was used to assess the statistical significance. All data are shown as mean±SD (triplicate tests).

Results

Biosynthesis of glucosinolate in Chinese cabbage sprouts grown under light conditions

A significant decrease in the total glucosinolate content was observed between the control (144.01 µmol/g DW) and all NaCl treatments (50.19–55.17 µmol/g DW, with no significant differences among the 50, 100, 150, and 200 mM levels, suggesting a threshold-type suppression at the lowest salt dose). Glucoraphanin, glucobrassicinapin and neoglucobrassicin decreased significantly and steadily with increasing NaCl (e.g., neoglucobrassicin decreased ~67%, from 11.26 to 3.70 µmol/g DW, between all pairs) while the other individual compounds (sinigrin and glucoalyssin) were fairly constant, except for a significant decrease only at the highest salt concentration (200 mM). Overall, the comparisons of the treatments revealed that NaCl does not consistently reduce the biosynthesis of glucosinolates, but rather changes the profile of the glucosinolates in a way that favors the production of some indolic glucosinolates at higher salt concentrations while progressively decreasing the biosynthesis of both aliphatic and other indolic glucosinolates (Table 1).

Biosynthesis of glucosinolate in Chinese cabbage sprouts grown under dark conditions

Total glucosinolate content in dark grow tomato decreased significantly from the control (108.60 µmol/g DW) to 50–150 mM NaCl (about 57–59% lower than control), but then increased significantly at 200 mM to 80.78 µmol/g DW (about 74% of the control). This U shaped dose dependent recovery was seen for several individual compounds, with glucoraphanin, gluconapin, glucobrassicinapin and neoglucobrassicin all dipping down sharply at 50–150 mM but recovering markedly at 200 mM, and gluconapin and neoglucobrassicin almost reaching control levels at the peak of the salt concentration. In contrast, glucobrassicin and 4-hydroxyglucobrassicin increased progressively and significantly across the NaCl gradient (glucobrassicin rising more than 4-fold, from 0.89 to 4.06 µmol/g DW, mainly driven by the jump from 100 to 150 mM and 150 to 200 mM), while glucoerucin declined steadily and significantly at every step (4.63→3.54→3.48→3.02→2.15 µmol/g DW). Sinigrin and glucoalyssin rose modestly but significantly above control levels at all NaCl concentrations and remained statistically stable among the salt treatments themselves, gluconasturtiin showed a non-significant upward trend peaking at 150 mM, and 4-methoxyglucobrassicin showed no significant differences across any treatment. Overall, comparing treatment to treatment shows that under dark conditions NaCl causes an initial sharp suppression of most glucosinolates (especially the dominant aliphatic compounds glucoraphanin and gluconapin) at 50–150 mM,

followed by a distinct high-salt (200 mM) recovery phase that is not observed in the light-grown sprouts, alongside a consistent, dark-independent rise in glucobrassicin and 4-hydroxyglucobrassicin with increasing salinity (Table 2).

Biosynthesis of carotenoid in Chinese cabbage sprouts grown under light conditions

Total carotenoid content declined progressively and significantly at every NaCl step under light conditions — 242.96 (0 mM) → 213.56 (50 mM) → 189.71 (100 mM) → 160.02 (150 mM) → 129.88 $\mu\text{g/g DW}$ (200 mM) — representing a steady, dose-dependent loss with no plateau, unlike the glucosinolate data, and culminating in a ~47% reduction at the highest salt level relative to control. The most abundant carotenoid (β -Carotene) exhibited a strictly monotonic decrease in all five treatments (99.94 to 84.11 to 74.10 to 64.09 to 52.20 $\mu\text{g/g DW}$), with each treatment being statistically different from the others, and accounting for the most of the total carotenoid loss. Lutein, the second most abundant carotenoid, did not significantly change from 0 to 50 mM (111.47 vs. 104.35 $\mu\text{g/g DW}$) but was significantly and progressively reduced beyond this concentration (93.23 vs. 74.88 vs. 57.41 $\mu\text{g/g DW}$ at 100, 200 and 300 mM, respectively), suggesting delayed but ultimately high salt sensitivity. The amounts of both violaxanthin and 9-cis- β -carotene decreased significantly with increasing NaCl, 9-cis- β -carotene leveling off between 100 and 150 mM

(14.2 vs. 13.64 not significant), and violaxanthin, although this was a minor component, experiencing the highest relative decrease (~80%, from 3.02 to 0.60 $\mu\text{g/g DW}$) of all carotenoids. Zeaxanthin decreased somewhat and was not significantly different from treatments beyond 50 mM NaCl, whereas 13 cis β carotenes and α carotenes did not differ significantly from any other NaCl level, implying that these minor carotenoids are not sensitive to NaCl level. In conclusion, the effect of NaCl on carotenoid biosynthesis in light grown sprouts is generally uniform, concentration dependent and suppressive, reducing the levels of all major carotenoids (β -carotene, lutein, violaxanthin, 9-cis- β -carotene), with none exhibiting the same biphasic response as some glucosinolates, as concentration of NaCl increases (Table 3).

Carotenoid biosynthesis in Chinese cabbage sprouts grown under dark conditions

The total carotenoid content in dark-grown sprouts demonstrated a distinct trend from light, being somewhat lower at the beginning, but then significantly lower as the salt concentration increased: 67.1 (50 mM), 56.08 (100 mM), 46.46 (150 mM), and 39.75 $\mu\text{g/g DW}$ (200 mM), with 200 mM representing a ~36% net reduction compared with the control value. This low stimulus was also reflected by lutein (the major carotenoid under dark conditions), which significantly increased from 47.57 to 56.19 $\mu\text{g/g DW}$ at

Table 1: Effects of NaCl concentration on glucosinolate biosynthesis in Chinese cabbage sprouts grown under light conditions

Trivial name	Individual glucosinolate content ($\mu\text{mol/g DW}$)				
	NaCl 0	NaCl 50	NaCl 100	NaCl 150	NaCl 200
Glucoraphanin	48.15 $\pm$ 0.01 ^a	14.48 $\pm$ 2.84 ^b	14.15 $\pm$ 0.68 ^b	14.00 $\pm$ 0.61 ^b	9.99 $\pm$ 0.68 ^c
Sinigrin	0.95 $\pm$ 0.02 ^a	0.86 $\pm$ 0.32 ^a	0.96 $\pm$ 0.06 ^a	0.89 $\pm$ 0.01 ^a	0.66 $\pm$ 0.07 ^b
Glucoalyssin	1.36 $\pm$ 0.09 ^a	1.07 $\pm$ 0.30 ^{bc}	1.21 $\pm$ 0.07 ^{ab}	1.23 $\pm$ 0.03 ^{ab}	0.94 $\pm$ 0.17 ^c
Gluconapin	54.55 $\pm$ 0.20 ^a	13.61 $\pm$ 1.64 ^d	13.44 $\pm$ 1.85 ^d	18.15 $\pm$ 1.54 ^c	21.51 $\pm$ 1.55 ^b
4-Hydroxyglucobrassicin	0.24 $\pm$ 0.05 ^c	0.29 $\pm$ 0.07 ^d	0.47 $\pm$ 0.02 ^c	0.57 $\pm$ 0.01 ^b	0.77 $\pm$ 0.01 ^a
Glucobrassicinapin	8.74 $\pm$ 0.78 ^a	1.90 $\pm$ 0.50 ^{bc}	1.62 $\pm$ 0.54 ^c	2.50 $\pm$ 0.11 ^b	2.18 $\pm$ 0.13 ^{bc}
Glucoerucin	4.98 $\pm$ 0.18 ^a	2.35 $\pm$ 0.67 ^{cd}	2.54 $\pm$ 0.07 ^c	3.07 $\pm$ 0.36 ^b	1.98 $\pm$ 0.03 ^d
Glucobrassicin	1.20 $\pm$ 0.20 ^c	0.93 $\pm$ 0.25 ^d	1.27 $\pm$ 0.04 ^c	1.98 $\pm$ 0.10 ^b	3.25 $\pm$ 0.03 ^a
4-Methoxyglucobrassicin	5.96 $\pm$ 0.38 ^a	5.47 $\pm$ 0.43 ^b	5.63 $\pm$ 0.45 ^{ab}	3.98 $\pm$ 0.32 ^c	3.18 $\pm$ 0.01 ^d
Gluconasturtiin	2.52 $\pm$ 1.51 ^a	0.95 $\pm$ 0.01 ^b	1.00 $\pm$ 0.01 ^b	1.66 $\pm$ 0.64 ^{ab}	1.58 $\pm$ 0.73 ^{ab}
Neoglucobrassicin	11.26 $\pm$ 0.67 ^a	5.94 $\pm$ 0.33 ^b	5.34 $\pm$ 0.82 ^b	4.41 $\pm$ 0.63 ^c	3.70 $\pm$ 0.25 ^c
Total	144.01 $\pm$ 3.81 ^a	50.19 $\pm$ 8.04 ^b	50.20 $\pm$ 4.30 ^b	55.17 $\pm$ 2.03 ^b	51.40 $\pm$ 3.48 ^b

Values are represented as the mean $\pm$ SD, and the superscripts of different letters (a, b, c, d, and e) indicate the significant differences (Duncan's multiple range test, $p < 0.05$)

Table 2: Effects of NaCl concentration on glucosinolate biosynthesis in Chinese cabbage sprouts grown under dark conditions

Trivial name	Individual glucosinolate content ($\mu\text{mol/g DW}$)				
	NaCl 0	NaCl 50	NaCl 100	NaCl 150	NaCl 200
Glucoraphanin	31.29 $\pm$ 6.48 ^a	11.30 $\pm$ 1.33 ^c	11.43 $\pm$ 0.82 ^c	9.74 $\pm$ 0.23 ^c	15.51 $\pm$ 0.73 ^b
Sinigrin	0.64 $\pm$ 0.15 ^b	1.17 $\pm$ 0.21 ^a	1.18 $\pm$ 0.27 ^a	1.00 $\pm$ 0.04 ^a	1.12 $\pm$ 0.17 ^a
Glucoalyssin	1.28 $\pm$ 0.00 ^c	1.83 $\pm$ 0.21 ^a	1.87 $\pm$ 0.28 ^a	1.57 $\pm$ 0.02 ^b	1.53 $\pm$ 0.05 ^b
Gluconapin	40.02 $\pm$ 10.21 ^a	9.33 $\pm$ 2.21 ^c	10.25 $\pm$ 3.47 ^c	12.20 $\pm$ 1.66 ^c	32.21 $\pm$ 0.70 ^b
4-Hydroxyglucobrassicin	0.24 $\pm$ 0.01 ^b	0.30 $\pm$ 0.08 ^b	0.24 $\pm$ 0.04 ^b	0.52 $\pm$ 0.04 ^a	0.60 $\pm$ 0.18 ^a
Glucobrassicinapin	5.59 $\pm$ 0.53 ^a	1.28 $\pm$ 0.62 ^c	1.42 $\pm$ 0.11 ^c	1.71 $\pm$ 0.78 ^c	3.72 $\pm$ 0.03 ^b
Glucoerucin	4.63 $\pm$ 1.15 ^a	3.54 $\pm$ 0.25 ^b	3.48 $\pm$ 0.23 ^b	3.02 $\pm$ 0.79 ^b	2.15 $\pm$ 0.45 ^c
Glucobrassicin	0.89 $\pm$ 0.12 ^c	1.02 $\pm$ 0.02 ^c	0.96 $\pm$ 0.15 ^c	1.62 $\pm$ 0.27 ^b	4.06 $\pm$ 0.78 ^a
4-Methoxyglucobrassicin	3.77 $\pm$ 1.94	4.49 $\pm$ 0.03	3.81 $\pm$ 0.11	3.30 $\pm$ 0.43	3.76 $\pm$ 0.96
Gluconasturtiin	1.45 $\pm$ 0.50 ^b	1.89 $\pm$ 0.07 ^b	2.39 $\pm$ 0.74 ^{ab}	3.60 $\pm$ 2.59 ^a	2.63 $\pm$ 0.08 ^{ab}
Neoglucobrassicin	13.19 $\pm$ 4.64 ^a	5.09 $\pm$ 2.36 ^b	5.68 $\pm$ 2.28 ^b	4.50 $\pm$ 1.43 ^b	11.06 $\pm$ 1.69 ^a
Total	108.60 $\pm$ 20.95 ^a	45.03 $\pm$ 7.54 ^c	46.69 $\pm$ 5.92 ^c	46.17 $\pm$ 9.01 ^c	80.78 $\pm$ 4.30 ^b

Values are represented as the mean $\pm$ SD, and the superscripts of different letters (a, b, c, and d) indicate the significant differences (Duncan's multiple range test, $p < 0.05$), and rows without superscripts indicate no statistical significance

50 mM, but significantly decreased to control levels (45.64) at 100 mM and further at 150 and 200 mM (37.71 and 32.4 $\mu\text{g/g DW}$, respectively). The responses of α -carotene and β -carotene with respect to concentration were the most irregular and non-monotonic, with both decreasing from control to 50 mM and recovering at 100 mM, before again decreasing at 200 mM (α -carotene: 0.76 $\rightarrow$ 0.13, not significant; 0.34 $\rightarrow$ 0.20 $\rightarrow$ 0.10 $\mu\text{g/g DW}$, all significant; β -carotene: 6.99 $\rightarrow$ 4.03 $\mu\text{g/g DW}$, all significant). The response of zeaxanthin was similar: a non-significant increase at 50 mM followed by significant decreases from 150 mM onward (0.51 $\rightarrow$ 0.60, not significant; 0.36, 0.22 $\mu\text{g/g DW}$, both significant); the response of the violaxanthin was similar, with significant decreases seen only at the extremes (2.20 vs. 0.91 $\mu\text{g/g DW}$, 0 vs. 200 mM). Comparing all treatments to all treatments shows that under dark conditions the situation with NaCl was very different, first a low dose (50 mM) effect of stimulation for lutein, zeaxanthin and total carotenoids, followed by a progressive, dose dependent suppression in the higher NaCl levels, indicating that etiolated tissue may buffer or even stimulate carotenoid biosynthesis at a mild salinity, but be suppressed at a more severe osmotic/ionic stress (Table 4).

Discussion

The biosynthesis, classification (aliphatic, indolic, aromatic) and metabolic fate of glucosinolates have been well characterized in Brassicaceae (Blažević *et al.*, 2020), and they are structurally diverse sulfur and nitrogen containing secondary metabolites. The total glucosinolate content of the present study dropped dramatically at the lowest NaCl concentration tested (50 mM) and did not continue to decrease further in a simple linear manner,

suggesting that even low levels of salinity are adequate to cause significant metabolic reallocation away from the production of glucosinolates. This follows previous reports of NaCl affecting the total glucosinolate content in broccoli sprouts (Guo *et al.*, 2013), and findings that exposure to light and NaCl together influence the glucosinolate, phenolic, and antioxidant profiles of the Brassica microgreens more broadly (Maina *et al.*, 2021), which had a light $\times$ NaCl factorial experimental design similar to that used here. Related evidence indicates that the effects of salt-associated elicitors (CaSO_4) also modify the nutritional profile of broccoli microgreens when exposed to NaCl stress, suggesting that exposure to NaCl reliably perturbs glucosinolate metabolism in both Brassica microgreen and sprout systems (Zeng *et al.*, 2022). The apparent suppressive effect of NaCl on the overall glucosinolate content, however, is shown to be a highly dynamic qualitative remodeling of the glucosinolate profile in the individual-compound data presented in the present study: dominant aliphatic glucosinolates (glucoraphanin, glucobrassicinapin, neoglucobrassicin) decreased as the NaCl increased in both light- and dark-grown sprouts, while levels of glucobrassicin and 4-hydroxyglucobrassicin increased progressively, suggesting a selective activation of the indolic branch of the pathway. The observed compositional change in response to NaCl stress can be interpreted as a consequence of a shift in stress-signaling pathways, instead of simply being a reduction in growth, as reported for the selective reshaping of glucosinolate and pigment accumulation in Brassica sprouts following jasmonate-related elicitation (Ortega-Hernández *et al.*, 2022).

Clearly, there was a difference between the light- and dark-grown sprouts at the highest NaCl concentration (200 mM). In the light, total glucosinolate levels were not

Table 3: Effects of NaCl concentration on carotenoid biosynthesis in Chinese cabbage sprouts grown under light conditions

	Individual carotenoid content ($\mu\text{g/g DW}$)				
	NaCl 0	NaCl 50	NaCl 100	NaCl 150	NaCl 200
Violaxanthin	3.02 $\pm$ 0.10 ^a	2.16 $\pm$ 0.36 ^b	1.75 $\pm$ 0.49 ^{bc}	1.23 $\pm$ 0.27 ^c	0.60 $\pm$ 0.10 ^d
Lutein	111.47 $\pm$ 7.96 ^a	104.35 $\pm$ 8.54 ^a	93.23 $\pm$ 3.47 ^b	74.88 $\pm$ 0.55 ^c	57.41 $\pm$ 3.28 ^d
Zeaxanthin	0.25 $\pm$ 0.02 ^a	0.23 $\pm$ 0.02 ^{ab}	0.21 $\pm$ 0.02 ^{ab}	0.20 $\pm$ 0.00 ^b	0.20 $\pm$ 0.04 ^b
13-cis- β -carotene	7.20 $\pm$ 2.29	6.31 $\pm$ 2.28	5.54 $\pm$ 1.68	5.33 $\pm$ 1.83	5.85 $\pm$ 0.69
α -Carotene	0.96 $\pm$ 0.09	0.77 $\pm$ 0.09	0.68 $\pm$ 0.05	0.65 $\pm$ 0.05	0.85 $\pm$ 0.47
β -Carotene	99.94 $\pm$ 2.27 ^a	84.11 $\pm$ 0.70 ^b	74.10 $\pm$ 3.70 ^c	64.09 $\pm$ 2.45 ^d	52.20 $\pm$ 3.16 ^c
9-cis- β -carotene	20.12 $\pm$ 1.00 ^a	15.63 $\pm$ 0.75 ^b	14.2 $\pm$ 1.19 ^{bc}	13.64 $\pm$ 0.90 ^c	12.77 $\pm$ 1.05 ^c
Total	242.96 $\pm$ 12.03 ^a	213.56 $\pm$ 8.80 ^b	189.71 $\pm$ 6.45 ^c	160.02 $\pm$ 1.92 ^d	129.88 $\pm$ 5.79 ^c

Values are represented as the mean $\pm$ SD, and the superscripts of different letters (a, b, c, d, and e) indicate the significant differences (Duncan's multiple range test, $p < 0.05$), and rows without superscripts indicate no statistical significance

Table 4: Effects of NaCl concentration on carotenoid biosynthesis in Chinese cabbage sprouts grown under dark conditions

Treatment	Individual carotenoid content ($\mu\text{g/g DW}$)				
	NaCl 0	NaCl 50	NaCl 100	NaCl 150	NaCl 200
violaxanthin	2.20 $\pm$ 0.47 ^a	1.67 $\pm$ 0.82 ^{ab}	1.60 $\pm$ 0.52 ^{ab}	1.46 $\pm$ 0.24 ^{ab}	0.91 $\pm$ 0.11 ^b
Lutein	47.57 $\pm$ 6.73 ^b	56.19 $\pm$ 4.50 ^a	45.64 $\pm$ 2.75 ^b	37.71 $\pm$ 0.60 ^c	32.4 $\pm$ 2.74 ^c
Zeaxanthin	0.51 $\pm$ 0.17 ^{ab}	0.60 $\pm$ 0.06 ^a	0.50 $\pm$ 0.06 ^{ab}	0.36 $\pm$ 0.03 ^{bc}	0.22 $\pm$ 0.04 ^c
13-cis- β -carotene	1.57 $\pm$ 0.46 ^a	1.11 $\pm$ 0.16 ^{ab}	1.14 $\pm$ 0.27 ^{ab}	1.16 $\pm$ 0.04 ^{ab}	0.79 $\pm$ 0.24 ^b
α -Carotene	0.76 $\pm$ 0.10 ^a	0.13 $\pm$ 0.04 ^c	0.34 $\pm$ 0.10 ^b	0.20 $\pm$ 0.04 ^c	0.10 $\pm$ 0.02 ^c
β -Carotene	6.99 $\pm$ 0.41 ^a	5.58 $\pm$ 0.15 ^b	5.03 $\pm$ 0.62 ^b	4.16 $\pm$ 0.43 ^c	4.03 $\pm$ 0.22 ^c
9-cis- β -carotene	2.45 $\pm$ 0.27 ^a	1.82 $\pm$ 0.08 ^b	1.83 $\pm$ 0.41 ^b	1.41 $\pm$ 0.2b ^c	1.30 $\pm$ 0.08 ^c
Total	62.05 $\pm$ 6.32 ^{ab}	67.1 $\pm$ 5.17 ^a	56.08 $\pm$ 2.05 ^b	46.46 $\pm$ 1.02 ^c	39.75 $\pm$ 2.64 ^c

Values are represented as the mean $\pm$ SD, and the superscripts of different letters (a, b, and c) indicate the significant differences (Duncan's multiple range test, $p < 0.05$)

significantly different from the 50-150mM treatments, but in the dark, total glucosinolate levels rose significantly to 200mM, close to 74% of the control value. The light-dependent divergence aligns with other evidence that light conditions and light exposure duration significantly impact the accumulation of beneficial vs. harmful phytochemicals in Brassica sprouts compared to un-sprouted counterparts (Paško *et al.*, 2019), and that the photoperiod alone significantly influenced glucosinolate accumulation patterns in Chinese kale sprouts under varying light conditions (Chen *et al.*, 2021). Characteristic of etiolated (dark-grown) seedlings, the investment of resources in elongation of hypocotyls and osmotic adjustment rather than into accumulation of photosynthetic pigments may influence the balance between metabolic sinks for growth and stress under high salinity, and the absence of the photosynthesis-derived reactive oxygen species (ROS) during darkness may alter this balance, permitting the shift of carbon and sulfur flux back to glucosinolate biosynthesis once initial acclimation is complete. This finding highlights the need to avoid directly extrapolating salinity-glucosinolate relationships solely based on light-grown tissue (Guo *et al.*, 2013; Maina *et al.*, 2021) and the importance of the photomorphogenic status of the sprouts in salt-elicitation experiments for Brassica.

The changes in the amounts of carotenoids in response to light conditions were not as compositional, but occurred in a monotonic manner along the entire NaCl gradient, and all 4 carotenoids decreased together as the NaCl increased. This broadly uniform suppression is in line with the fact that the biosynthesis of carotenoids in Brassica sprouts is very responsive to environmental and light-related inputs: carotenoid and glucosinolate pools have been shown to change together under different light-emitting diode (LED) regimes in rapeseed sprouts and seedlings (Groenbaek *et al.*, 2018) and that combined abiotic elicitors (UV radiation, methyl jasmonate) cause simultaneous changes in biosynthesis of glucosinolates, phenolics, carotenoids and chlorophyll in broccoli sprouts (Moreira-Rodríguez *et al.*, 2017), suggesting a metabolic and regulatory linkage between carotenoid and glucosinolate pathways, and not independence, in the context of stress. Carotenoids decrease in light-grown sprouts as the salt concentration increases, which could be due to a trade-off between depletion of carotenoids as antioxidant resources and re-synthetic capabilities under light and salt induced oxidative stress.

Total carotenoid content, however, and, in particular, lutein and zeaxanthin exhibited a bimodal (up and down) response to NaCl, with a moderate increase at 50 mM NaCl followed by a decrease at higher concentrations. The observation of targeted elicitation (e.g., selenium, sulfur, and methyl jasmonate) enhancing lutein production and accumulation, as well as low-dose salinity, could give a similar low dose stimulation to lutein production that is observed in this study, and thus, it appears as though mild stress inputs may temporarily favor xanthophyll production before more severe stress overcomes all xanthophyll production. However, at higher NaCl concentrations (100-200 mM), this buffering capacity was exceeded and

carotenoid levels dropped in a similar manner as in light, suggesting that this light-induced stimulation of protection is restricted to a narrow salinity window in the dark.

Combined, these results suggest that light environment has a fundamental influence on the expression of secondary metabolism (glucosinolates and carotenoids) and defense (glucosinolates) responses of Chinese cabbage sprouts, and that the light itself could serve as an elicitor for the production of secondary metabolites in plant tissues, more broadly (Murthy *et al.*, 2024), as well as induce secondary metabolism in horticultural crops (Xu *et al.*, 2021; Trivellini *et al.*, 2023). Light caused a long-lasting compositionally shifted suppression of glucosinolates with quantitatively stable results and a strictly dose-dependent decline of carotenoids. Both glucosinolates and carotenoids exhibited non-monotonic (biphasic) responses under dark conditions, suggesting a more complex and stage-specific metabolic reprogramming under dark conditions in etiolated tissue. The second finding is consistent with other evidence, which suggested that the best NaCl concentration for accumulation of glucosinolates in Brassica sprouts varies with the species, under both light and dark cultivation conditions (Guijarro-Real *et al.*, 2022), supporting the findings of the applied research.

Conclusion

In conclusion, the concentration of NaCl and light regime interact, rather than independently, on the accumulation and composition of glucosinolates and carotenoids in Chinese cabbage sprouts. Under light conditions, NaCl caused a significant long-term reduction in the total glucosinolates (glucosinolates and their degradation products) and a dose-dependent decrease in carotenoids, while under dark conditions the responses of both the metabolite classes were biphasic, non-monotonic, involving a strong recovery of glucosinolates and a transient stimulation of carotenoids for specific NaCl concentrations. NaCl did not overall reduce glucosinolate levels, but rather altered the qualitative profile, enriching the production of indolic glucosinolates (glucobrassicin, 4-hydroxyglucobrassicin) and reducing the production of aliphatic glucosinolates (glucoraphanin) that dominated the profile. Based on these results, moderate NaCl treatment (50 mM) in combination with dark growth conditions could provide a potential non-genetic elicitation approach to increase the indolic glucosinolates in Chinese cabbage sprouts; the light-grown sprouts could be better grown for higher carotenoid production under low-salinity conditions. Future studies incorporating transcriptomic and enzymatic analyses are recommended to elucidate the molecular basis of these light-dependent salinity responses and to optimize NaCl application protocols for functional sprout production.

Author contributions

Minhwan Lee: Methodology, Formal analysis, Writing – original draft. Chanung Park: Data curation, Formal analysis, Methodology. Nam Su Kim: Formal analysis, Data curation. Md Romij Uddin: Data curation, Formal analysis. Ramaraj

Sathasivam: Data curation, Formal analysis, Methodology, Writing – review & editing. Haenghoon Kim: Data curation, Formal analysis. Sang Un Park: Conceptualization, Investigation, Validation, Visualization, Funding, Writing – review & editing. All authors approved the final manuscript.

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