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Exposure time and cultivar modulate supplementary UVA and/or UVB radiation impact on yield components, mineral profile, and phytonutrient content of pea shoots

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ABSTRACT

Although representing a small proportion of solar radiation, ultraviolet (UV) radiation (280–400 nm) has been shown to greatly affect growth, photomorphogenesis, and secondary metabolism in plants. Given the implications to crop physiology and nutritional quality, there is interest in understanding the effects of supplemental UVA and UVB radiation on the growth and phytonutrient content of nutrient-dense crops, like microgreens. We conducted a greenhouse study to evaluate the effect of supplemental UVA, UVB, and combined UVAB radiation on yield, mineral profiles, and antioxidant components of two varieties of pea (*Pisum sativum* L.) microgreens: 'Field Pea' and 'Dwarf Grey Sugar Pea.' After full germination, pea shoots were exposed to sunlight for one day and then were exposed to supplemental treatments of UVA (1.83 W/m^2), UVB (0.61 W/m^2), or UVA (1.55 W/m^2) + UVB (0.61 W/m^2) radiation for 3-, 6-, or 12-h/day for 6 days. The supplementary UVA treatment significantly increased fresh yield and dry weight in pea microgreens, with 12-h of UVA having the highest yield. Conversely, exposure to supplementary UVB and UVAB produced a loss in yield with all exposure times above 3-h/day. Exposure to UVA radiation had no significant effect on total phenolic content (TPC) and total antioxidant activity (TAA), while the exposure to UVB and UVAB radiation showed a significant decrease of both TPC and TAA with exposure times above 3-h/day. UVB supplementary radiation reduced pea shoot mineral accumulation, while UVA positively influenced mineral content only in 'Dwarf Grey Sugar Pea'. These results suggest that exposure to supplementary UVB radiation (0.61 W/m^2) for longer than 3-h/day, regardless of the exposure to UVA radiation, results in significant losses in yield and antioxidant synthesis in pea microgreens.

1. Introduction

Both current global climate change and the increased threat of global catastrophic risks (GCRs), such as a "nuclear winter," pose many known and unknown risks to global agriculture and food production [1–5]. The ongoing Ukraine-Russia conflict, Israel-Hamas War, and increased threats of nuclear war, yet again make global nuclear war and post-war "nuclear winter" a tangible risk to be analyzed [6]. Current models predict that a global nuclear war to result in a significantly drier, colder, and darker global climate for years after the event, accompanied by increased UV radiation several years post-nuclear war [1,7]. Additionally, climate change is currently causing shifts in UV radiation globally with some areas experiencing increased UV radiation, while others are experiencing a decrease [8].

One of the shared risks for both GCRs and current global climate change is an increase in ground-level UV radiation [6]. After a nuclear conflict, when soot clouds dissipate, allowing the global climate to return to near normal conditions, models predict a significant increase in ultraviolet (UV) radiation (280–400 nm). Naturally, the ozone layer filters out all of the UVC (100–280 nm) radiation and 95 % of UVB (280–315 nm) radiation [9]. Regardless of any potential GCR, the intensity of UVB wavebands at ground level changes based on atmospheric conditions, predominantly influenced by the ozone layer. The Montreal Protocol, put in place over 40 years ago, was successful in restrengthening the ozone layer by cutting down harmful emissions [10,11]; however, risks of increased UV radiation still remain due to climate

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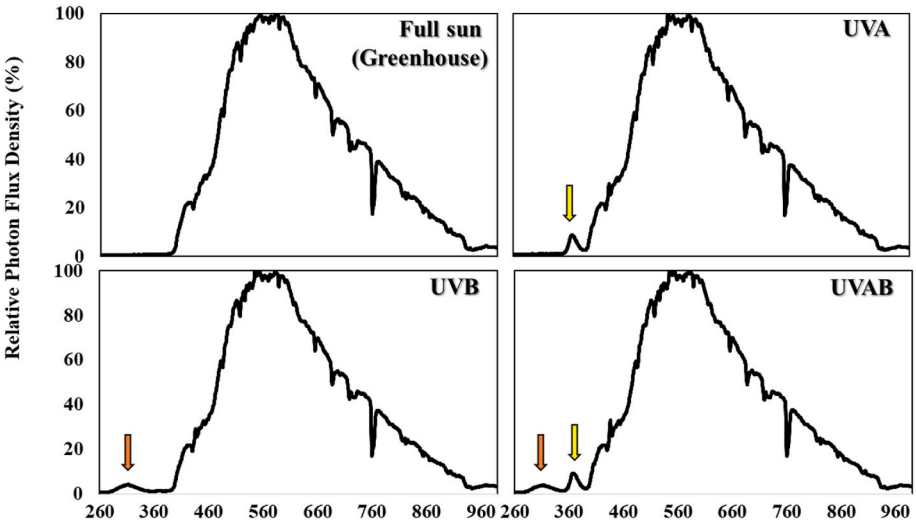

Fig. 1. Relative photon flux density (%) recorded in the greenhouse at different wavelengths (nm) without supplementary radiation (control) and with supplementary UVA, UVB and UVAB radiation.

change fluctuations and GCRs [8,12].

Although representing only a small fraction of the solar radiation, UV radiation that reaches the surface of the Earth greatly affects plant growth, photomorphogenesis, and secondary metabolism. For example, UVB radiation has been shown to decrease growth rate and biomass production in many crops [13]. Generally, exposure to UVB radiation affects plant morphology by decreasing leaf area, increasing leaf thickness, decreasing petiole length, influencing the shape of inflorescence and leaves, as well as decreasing stem elongation [14]. Interestingly, exposure to UVA or UVB wavebands can cause opposite outcomes in different crop species [15]. For example, it has been shown that UV radiation responses differ between cultivars of the same species, indicating that generalizing UV radiation responses is inadvisable [16].

Increased UV radiation could be problematic due to the many negative effects described above. Conversely, small doses of UV radiation wavebands could elicit increased production of antioxidants and phenolic compounds, which in turn may improve the nutritional value of food plants rather than impacting plant growth and yield. Using basil as a test crop, a recent study revealed the existence of an inverse relationship between yield and nutritional content [16]. Evidence shows that UV radiation causes some plants to produce more flavonoids and other bioactive compounds in leaves, which are beneficial to human health [15]. Additionally, small amounts of supplemental UVB radiation have been shown to increase plants' tolerance to high-radiation stress [17]. Plants experience 10–100 times more UVA than UVB naturally, yet less is known about UVA radiation's impact on plant growth than that of UVB [12,18].

Given the implications in terms of plant physiology and nutritional quality, there is great interest in understanding the effects of differing supplemental UVA and UVB radiation exposure time and their combination on the growth and secondary metabolism of nutrient-dense crops like microgreens [19–21]. Additionally, the effects of the simultaneous exposure to UVA and UVB on crop growth are poorly understood, with few studies investigating their separate and combined effects [12]. Moreover, the response of plants to different doses of UVB radiation is not well understood either [14].

To better understand how increased exposure to UV radiation wavebands affect plants, a greenhouse study was conducted to evaluate the effect of supplementary UVA, UVB, and combined UVAB radiation on growth, physiology, and nutritional components of two varieties of pea (*Pisum sativum* L.) shoots: 'Field Pea' and 'Dwarf Grey Sugar Pea'. At harvest, yield components, chlorophyll, mineral profile and phytonutrient content of pea microgreens grown under UV radiation treatments were compared to a negative control. We hypothesize that increasing the time of exposure to supplementary UVB radiation may cause incremental damages to the plant affecting its primary and secondary metabolism, while increasing the time of exposure to supplementary UVA may have positive effects on plant growth but could reduce nutrient density, and when combining supplementary UVA and UVB radiation, UVA radiation could in part offset the detrimental effect of the UVB radiation on plants.

2. Materials & methods

2.1. Plant material, treatments, and experimental design

The study was conducted in a glasshouse (9.75 m × 16.8 m) at the Pennsylvania State University Greenhouse Facilities located at University Park (40°47′53.4″ N 77°51′35.8″ W), PA, in Central Pennsylvania over the spring of 2021. Pea (*Pisum sativum* L.) shoot seeds of two cultivars, 'Field Pea' and 'Dwarf Grey Sugar Pea', were purchased from Johnny's Selected Seeds (Winslow, ME, USA) and had 98 % and 97 % germinability, respectively. The two cultivars were selected based on their performance in previous studies [22,23].

The seeds of the two pea varieties were soaked in water for 12 h and then sown at a density of 1 seed/cm^2 in a peat-perlite mix (Sunshine Mix 4, Sun Gro Horticulture, Agawam, MA, USA) using 12 × 16-cm growing trays and grown under greenhouse condition in absence of light for three days. The growing mix contained Canadian sphagnum peat moss, perlite, dolomite lime, silicon, and a wetting agent. During germination, trays were misted with tap water once a day. After full germination, pea shoots were watered via subirrigation and while grown in the greenhouse were first exposed to solar radiation for one day (12 h of solar radiation) and then were exposed to supplemental UVA (315–400 nm; 1.83 W/m^2), UVB (280–315 nm; 0.61 W/m^2), and UVA (1.55 W/m^2) plus UVB (0.61 W/m^2) radiation (UVAB, 280–400 nm) for 3-, 6-, and 12-h/day (centered around noon) for 7 days. Exposure time to UVA and UVB radiation was selected based on preliminary experiments and considering the potential minimum and maximum exposure time to the UV radiation at different latitudes in a global post-catastrophic scenario [7,24]. UV radiation treatments were applied using fluorescent UV lamps (Actinic BL-TL-40W-10 UVA, TL-40W/12 UVB, Philips) activated at the defined time by timers. Fig. 1 illustrates for each radiation treatment, the relative photon flux density recorded using an Apogee Model PS-300 spectroradiometer equipped with a cosine-corrected detector and leveling fixture (Apogee Instruments, Logan, UT, USA). The

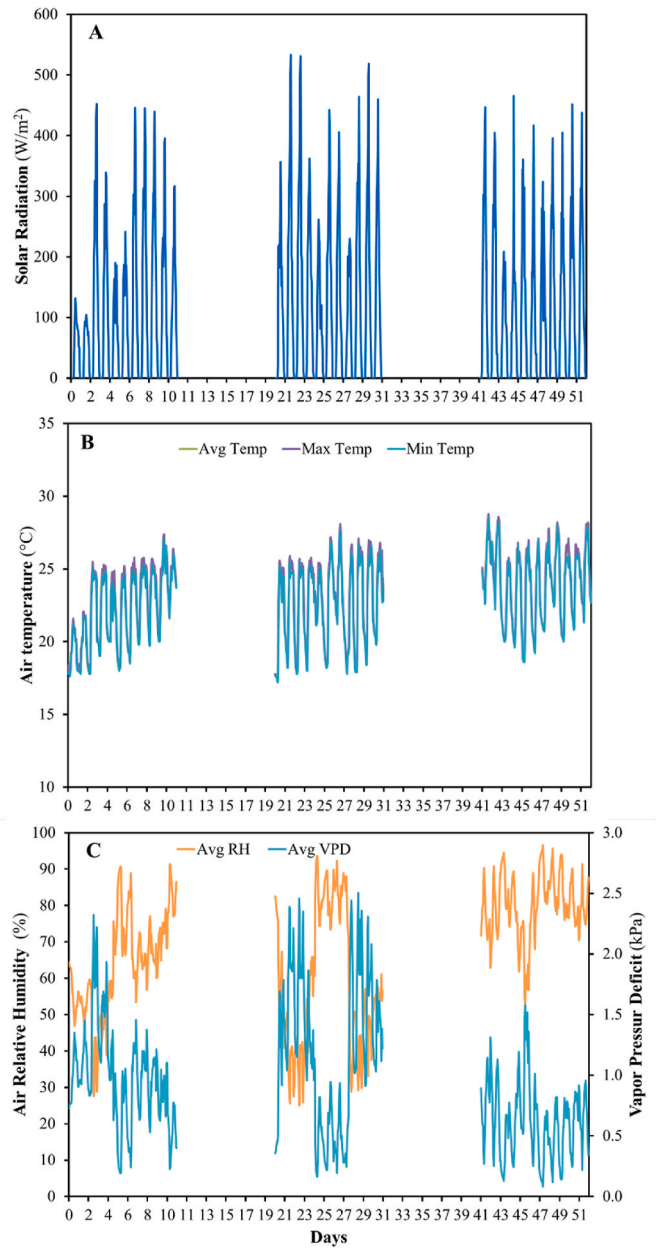

Fig. 2. Side-by-side comparison at harvest of 'Field Pea' and 'Dwarf Grey Sugar Pea' microgreens grown in presence of solar radiation not supplemented (control) or supplemented with UVA, UVAB, and UVB radiation for 3, 6, or 12 h per day.

experiment was repeated three times arranging treatments in a split-split-plot experimental design, with exposure time randomized within whole plots, supplementary UV radiation treatments randomized in sub-plots and pea cultivars randomized in sub-sub plots. During each growing cycle, solar radiation levels, air temperature, relative humidity and vapor pressure deficit were monitored and recorded through an Atmos 41 all-in-one weather station (Meter Group Inc., Pullman, WA). Daily solar radiation was on average 453, 534, and 466 W/m^2 (equivalent to 951, 1121, and 979 μmol/m^2/s photosynthetic photon flux density) during the three growing cycles, respectively (Fig. 2A). Daily air temperature in the greenhouse was on average 22.3, 22.8, and 24.0 °C during the first, second, and third growing cycle, respectively. Daily minimum and maximum air temperature ranged from 17.2 to 18.6 °C and from 27.4 to 28.8 °C, respectively (Fig. 2B). Over the three growing cycles, daily relative humidity in the greenhouse was on average 67.4 % and ranged between a minimum of 25.1 % and a maximum of 96.6 % (Fig. 2C). Vapor pressure deficit was on average 1, 1.2, and 0.6 kPa during the three growing cycles, respectively.

Table 1
Effect of UV supplementary radiation and time of exposure on the yield components of 'Field Pea' and 'Dwarf Grey Sugar Pea' microgreens.[a].

	Fresh yield (kg/m^2)	Shoot fresh weight (mg)	Dry weight (g/m^2)	Dry matter content (%)
Supplementary radiation (A)				
UVA	5.34 a	596.88 a†	444.15 a	8.33 b
UVAB	4.27 b†	468.53 b†	400.80 b†	9.49 a†
UVB	4.29 b†	468.41 b†	400.61 b†	9.44 a†
Time of exposure (B)				
3 h	5.03 a	558.68 a	426.25 a	8.46 c
6 h	4.74 b	523.19 b	419.73 a	8.95 b
12 h	4.13 c	451.94 c	399.57 b	9.85 a
Cultivar (C)				
'Field Pea'	4.53 b	488.90 b	388.85 b	8.72 b
'Dwarf Grey Sugar Pea'	4.73 a	533.65 a	441.52 a	9.45 a
A	***<0.0001***	***<0.0001***	***<0.0001***	***<0.0001***
B	***<0.0001***	***<0.0001***	***0.0005***	***<0.0001***
A × B	***<0.0001***	***<0.0001***	***<0.0001***	***<0.0001***
C	***<0.0001***	***<0.0001***	***<0.0001***	***<0.0001***
A × C	*0.63*	*0.63*	*0.17*	*0.70*
B × C	***0.008***	*0.16*	*0.06*	***0.01***
A × B × C	*0.12*	***0.03***	***0.02***	*0.31*
Control	5.27	567.83	435.36	8.38
Control vs UVA	*0.28*	***0.003***	*0.39*	*0.68*
Control vs UVAB	***<0.0001***	***<0.0001***	***0.001***	***<0.0001***
Control vs UVB	***<0.0001***	***<0.0001***	***0.001***	***<0.0001***

[a] Reported values are averages of three growth cycles and replications. P-values are reported in italics for the main effects and their interaction, as well as for the contrasts between the control (solar radiation with no supplementary UV radiation) and different treatment groups. P-values ≤0.05 are reported in bold indicating a significant difference. The following symbol † indicates a significant difference compared to the control using contrast in the linear mixed model.

At harvest, 11 days after sowing, pea shoot fresh yield (FY), average shoot fresh weight, and dry weight (DW) were measured on three growing trays per experimental unit. Subsamples of the pea shoots were oven-dried at 65 °C until constant weight to measure DW and dry matter (DM) content or were stored in a −80 °C and freeze-dried for the analysis of chlorophyll content, total phenolic compounds (TPC), and total antioxidant activity (TAA).

2.2. Mineral analysis

Oven-dried pea shoot samples were ground with a mill, sieved (1 mm) and sent to the Penn State Agricultural Analytical Services Laboratory at University Park, PA, for mineral analysis using the same methods described in Ref. [22]. Samples were analyzed for total nitrogen using dry combustion with an Elementar Max Cube in CN mode (Elementar Americas Inc., Ronkonkoma, NY) as described in Vecchia et al. (2020) and macrominerals (P, K, Ca, Mg, S, and Na) and microminerals (Mn, Fe, Cu, B, and Zn) were analyzed after acid digestion [25] using ICP-OES (Varian 730-ES, Agilent Technologies, Santa Clara, CA, USA). Green bean tissue (North American Proficiency Testing (NAPT) Plant standard tissue #2014-209) was used as positive control for data validation [26].

2.3. Chlorophyll content

Pea shoot total chlorophyll *a*, *b*, and total chlorophyll content were analyzed using the method explained by Porra et al. [27] with slight modifications [27,28]. This procedure was outlined by Poudel et al. [29]. Ground freeze-dried samples of 0.015 g were extracted with 1.5 mL of 80 % acetone for 25 min using an ultrasonic processor (Branson

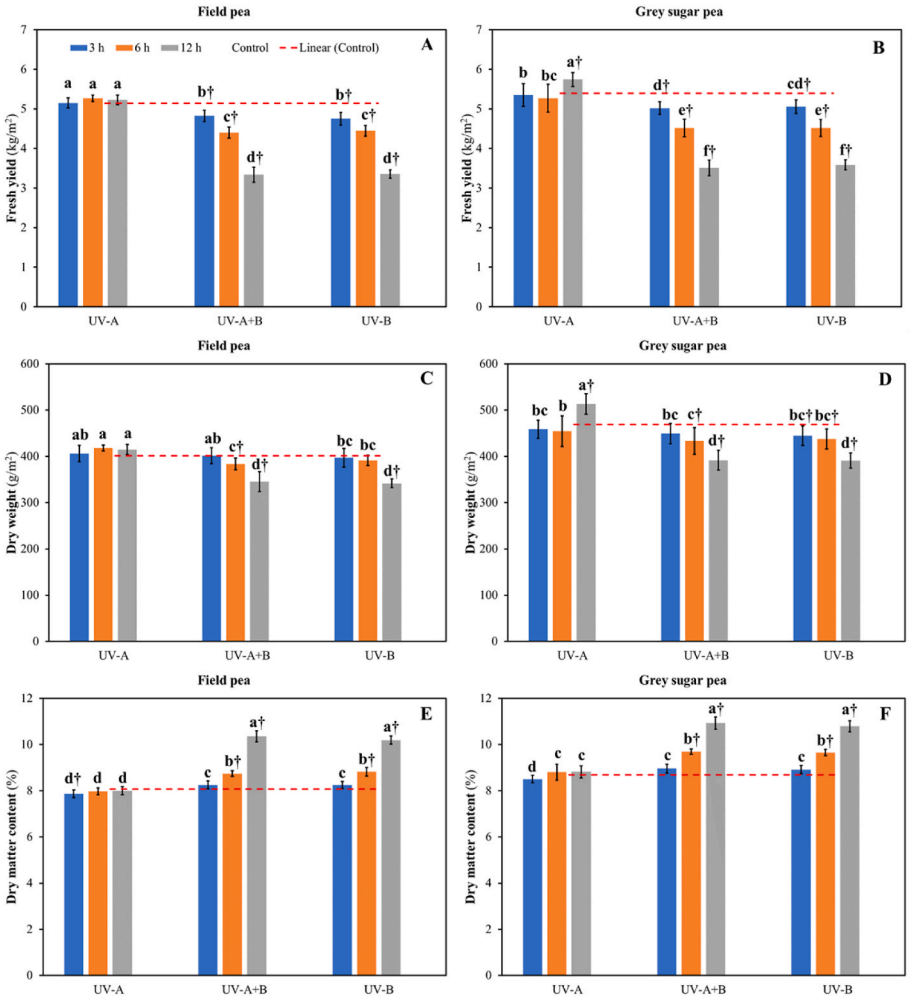

Fig. 3. Interaction effect of supplementary UV radiation and time of exposure on fresh yield (A, B), dry weight (C, D) and dry matter content (E, F) of 'Field Pea' (A, C, E) and 'Dwarf Grey Sugar Pea' (B, D, F) shoots. Vertical bars indicate average values and standard error (n = 3). Different letters indicate significant differences at p = 0.05 according to the Tukey test. The dashed line indicates the average value of the control (greenhouse solar radiation). † indicates a significant difference compared to the control using contrast in the linear mixed model.

CPX2800H, Branson Ultrasonics, Brookfield, CT) and a second time for additional 25 min with 100 vol of 80 % methanol. The sample was centrifuged at 4000×*g* for 5 min. The supernatant absorbance at 645 nm and 663 nm was recorded using a microplate reader (Synergy H1, BioTek, Winooski, VT).

2.4. Total phenols and antioxidant activity

Samples were analyzed for total phenolic compounds concentration using a modification of the Folin-Ciocalteu method [30,31]. Exact methods and materials are the same as [22]. Pulverized freeze-dried pea shoot samples of 0.04 g were extracted with 4 mL of 80 % methanol using a sonicator (Branson CPX2800H, Branson Ultrasonics, Brookfield, CT) for 20 min, followed by 20 s of vortexing. A portion (1.5 mL) of the extract was transferred to a microcentrifuge tube and stored overnight at 4 °C in a dark environment. Twelve hours later, the extract was centrifuged at 1000 rpm for 2 min. The supernatant of the sample extract (50 μL) was added to a microcentrifuge tube containing 135 μL of distilled water and 750 μL of Folin-Ciocalteu reagent, followed by 600 μL of Na_2CO_3. For the blank sample, 50 μL of 80 % methanol was used instead of the supernatant as described in detail by Mather et al. [26]. The mixture was vortexed for 10 s and incubated in a water bath at 45 °C for 20 min. Samples were left to cool down to room temperature, and then the absorbance was read at 765 nm using a microplate reader (Synergy H1, BioTek, Winooski, VT). Gallic acid was used as a standard, and the total phenol concentration of each sample was expressed as gallic acid equivalent (GAE) on a dry weight basis (mg GAE/g DW).

Total antioxidant activity was determined following the 2,2-diphenyl-1-picrylhydrazyl (DPPH) antioxidant assay described by Herald et al. [32] and Alrifai et al. [33] with slight modifications, as detailed by Mather et al. [26]. An aliquot (1.5-mL) of the same extract used for determining the total phenolic content was stored overnight at −20 °C. The following day, samples were centrifuged at 12,000×*g* for 2 min; 200 μL of the DPPH (350 mM in 80 % methanol) solution was combined with 25 μL of the samples or standard or 2525 μL of the 80 % methanol (used for reference to estimate the amount of DPPH quenched by samples or standard). For blank, 225 μL of 80 % methanol was added. The microplate was covered with parafilm and a lid and incubated in the dark at room temperature for 6 h, and the absorbance was read at 517 nm (Synergy H1, BioTek, Winooski, VT). Trolox (6-hydroxy-2,5,7,8-tetramethylchroman-2-carboxylic acid, 25–800 μM) was used as a standard for determining the total antioxidant activity, and the results were expressed as Trolox equivalent on a dry mass basis (mM TEAC/g DW).

2.5. Data analysis

All collected data were analyzed using a three-way analysis of variance (ANOVA) with the MIXED and GLIMMIX procedure in SAS Version

Table 2
Effect of UV supplementary radiation and time of exposure on the mineral content of 'Field Pea' and 'Dwarf Grey Sugar Pea' microgreens. [a].

	N	P	K	Ca	Mg	S	Fe	Zn	Mn	Cu	B	Na
	%						mg/kg					
Supplementary radiation (A)												
UVA	7.31 b	0.72 b	2.61 b	0.41	0.45	0.71 b	99.50 c	72.53 b†	45.11 b	13.94 b	15.36 b	606.83 a†
UVAB	7.91 a†	0.79 a†	2.75 a†	0.42	0.46	0.78 a†	110.25 a†	78.22 a†	49.58 a†	14.83 a†	17.03 a†	474.64 b†
UVB	7.94 a†	0.79 a†	2.71 a†	0.40	0.45	0.76 a†	107.31 b†	77.89 a†	47.58 ab†	15.11 a†	16.50 a	456.22 b†
Time of exposure (B)												
3 h	7.53 c	0.73 c	2.69	0.41	0.45	0.72 c	100.94 b	72.08 c	44.75 b	13.89 c	15.86 b	540.11 a
6 h	7.65 b	0.76 b	2.65	0.42	0.45	0.75 b	103.78 b	74.89 b	47.03 b	14.36 b	16.03 b	521.86 ab
12 h	7.98 a	0.81 a	2.73	0.41	0.45	0.79 a	112.33 a	81.67 a	50.50 a	15.64 a	17.00 a	475.72 b
Cultivar (C)												
'Field Pea'	7.34 b	0.69 b	2.65 b	0.48 a	0.48 a	0.72 b	105.17	75.56 b	49.06 a	15.22 a	16.89 a	516.61
'Dwarf Grey Sugar Pea'	8.10 a	0.84 a	2.73 a	0.35 b	0.42 b	0.78 a	106.20	76.87 a	45.80 b	14.04 b	15.70 b	508.52
A	***<0.0001***	***<0.0001***	***0.004***	*0.06*	*0.26*	***<0.0001***	***<0.0001***	***<0.0001***	***0.0003***	***0.001***	***<0.0001***	***<0.0001***
B	***<0.0001***	***<0.0001***	*0.09*	*0.74*	*0.55*	***<0.0001***	***<0.0001***	***<0.0001***	***<0.0001***	***<0.0001***	***<0.0001***	***0.01***
A × B	***<0.0001***	***<0.0001***	***0.002***	*0.55*	*0.14*	***0.0002***	***<0.0001***	***<0.0001***	*0.11*	***<0.0001***	***0.005***	***0.003***
C	***<0.0001***	***<0.0001***	***<0.0001***	***<0.0001***	***<0.0001***	***<0.0001***	*0.30*	***0.01***	***0.0003***	***<0.0001***	***<0.0001***	*0.66*
A × C	*0.20*	*0.32*	*0.06*	*0.27*	*0.68*	*0.28*	*0.12*	*0.82*	*0.51*	*0.17*	*0.10*	*0.97*
B × C	*0.14*	*0.59*	***0.002***	***0.005***	*0.15*	*0.41*	*0.40*	***0.005***	*0.79*	***0.02***	***0.02***	*0.39*
A × B × C	*0.71*	*0.58*	*0.54*	*0.32*	*0.10*	*0.72*	*0.22*	*0.58*	*0.49*	*0.72*	*0.23*	*0.22*
Control	7.38	0.72	2.63	0.42	0.46	0.69	97.67	69.83	42.17	13.75	15.92	546.33
Control vs UVA	*0.62*	*0.85*	*0.64*	*0.76*	*0.30*	*0.24*	*0.30*	***0.01***	*0.07*	*0.54*	*0.19*	***0.05***
Control vs UVAB	***0.0004***	***0.01***	***0.003***	*1.00*	*0.65*	***<0.0001***	***<0.0001***	***<0.0001***	***<0.0001***	***0.001***	***0.01***	***0.02***
Control vs UVB	***0.0002***	***0.01***	***0.04***	*0.55*	*0.17*	***<0.0001***	***<0.0001***	***<0.0001***	***0.001***	***<0.0001***	*0.17*	***0.005***

[a] Reported values are averages of three growth cycles and replications. P-values are reported in italics for the main effects and their interaction, as well as for the contrasts between the control (solar radiation with no supplementary UV radiation) and different treatment groups. P-values ≤0.05 are reported in bold indicating a significant difference. The following symbol † indicates a significant difference compared to the control using contrast in the linear mixed model.

Table 3
Effect of UV supplementary radiation and time of exposure on the mineral accumulation of 'Field Pea' and 'Dwarf Grey Sugar Pea' microgreens. [a].

	N	P	K	Ca	Mg	S	Na	Fe	Zn	Mn	Cu	B
	kg/m^2							g/m^2				
Supplementary radiation (A)												
UVA	32.30 a	3.20	11.51 a	1.80 a	1.98 a	3.14 a	0.27 a	43.88 a	32.06 a†	19.95 a†	6.14 a†	6.73 a
UVAB	31.10 b	3.11	10.77 b	1.65 b	1.79 b†	3.06 ab	0.19 b	43.14 ab	30.79 b	19.51 ab†	5.84 b	6.65 ab
UVB	31.15 b	3.09	10.60 b	1.59 b†	1.75 b†	3.01 b	0.18 b	41.99 b	30.56 b	18.70 b	5.92 b	6.41 b†
Time of exposure (B)												
3 h	31.17 b	3.02 b	11.11 a	1.67	1.86 a	2.98 b	0.23 a	41.68 b	29.85 b	18.48 b	5.73 b	6.55
6 h	32.11 a	3.19 a	11.09 a	1.75	1.88 a	3.14 a	0.22 ab†	43.47 a	31.53 a	19.82 a	6.03 a	6.65
12 h	31.28 ab	3.18 a	10.68 b	1.61	1.78 b	3.09 ab	0.20 b†	43.86 a	32.04 a	19.86 a	6.13 a	6.58
Cultivar (C)												
'Field Pea'	27.80 b	2.61 b	10.05 b	1.82 a	1.82	2.72 b	0.20 b	39.78 b	28.67 b	18.70 b	5.77 b	6.39 b
'Dwarf Grey Sugar Pea'	35.24 a	3.65 a	11.87 a	1.53 b	1.86	3.42 a	0.23 a	46.22 a	33.60 a	20.08 a	6.16 a	6.80 a
A	***0.001***	*0.13*	***0.001***	***<0.0001***	***<0.0001***	***0.01***	***<0.0001***	***0.02***	***0.01***	***0.01***	***0.003***	***0.03***
B	***0.02***	***0.001***	***0.01***	*0.07*	***0.002***	***0.01***	***0.03***	***0.004***	***<0.0001***	***0.03***	***<0.0001***	*0.72*
A × B	***0.0004***	*0.31*	***<0.0001***	***<0.0001***	***<0.0001***	***0.004***	***0.0002***	*0.14*	*0.62*	*0.18*	*0.52*	*0.09*
C	***<0.0001***	***<0.0001***	***<0.0001***	***<0.0001***	*0.10*	***<0.0001***	***0.002***	***<0.0001***	***<0.0001***	***<0.0001***	***<0.0001***	***0.0001***
A × C	***0.01***	*0.19*	***0.003***	*0.93*	*0.43*	*0.41*	*0.43*	***0.01***	*0.15*	***0.05***	*0.58*	*0.31*
B × C	*0.87*	*0.45*	*0.20*	***0.003***	*0.11*	*0.16*	*0.45*	*0.10*	***0.02***	*0.27*	***0.003***	***0.03***
A × B × C	*0.37*	*0.54*	*0.18*	*0.41*	*0.20*	*0.59*	*0.13*	*0.45*	*0.59*	*0.26*	*0.58*	*0.36*
Control	31.47	3.05	11.2	1.78	1.97	2.96	0.24	41.46	29.76	17.94	5.84	6.81
Control vs UVA	*0.56*	*0.47*	*0.44*	*0.81*	*0.76*	*0.17*	*0.08*	*0.11*	***0.04***	***0.003***	***0.04***	*0.69*
Control vs UVAB	*0.80*	*0.78*	*0.29*	*0.07*	***0.0001***	*0.46*	***0.01***	*0.27*	*0.36*	***0.02***	*1.00*	*0.41*
Control vs UVB	*0.83*	*0.83*	*0.15*	***0.01***	***<0.0001***	*0.70*	***0.004***	*0.73*	*0.47*	*0.25*	*0.59*	***0.05***

[a] Reported values are averages of three growth cycles and replications. P-values are reported in italics for the main effects and their interaction, as well as for the contrasts between the control (solar radiation with no supplementary UV radiation) and different treatment groups. P-values ≤0.05 are reported in bold indicating a significant difference. The following symbol † indicates a significant difference compared to the control using contrast in the linear mixed model.

9.4 software (SAS Institute, Cary, NC) to compare the effect of the supplementary radiation, the time of exposure to UV radiation and the two cultivars of pea shoots and the interactions between all three factors according to a factorial split-split-plot experimental design. Significant differences in means were separated using the Tukey test at $p < 0.05$. A series of contrasts was conducted using the GLIMMIX procedure in SAS 9.4 to determine differences between experimental treatments and the untreated control (solar radiation without supplementary UV radiation).

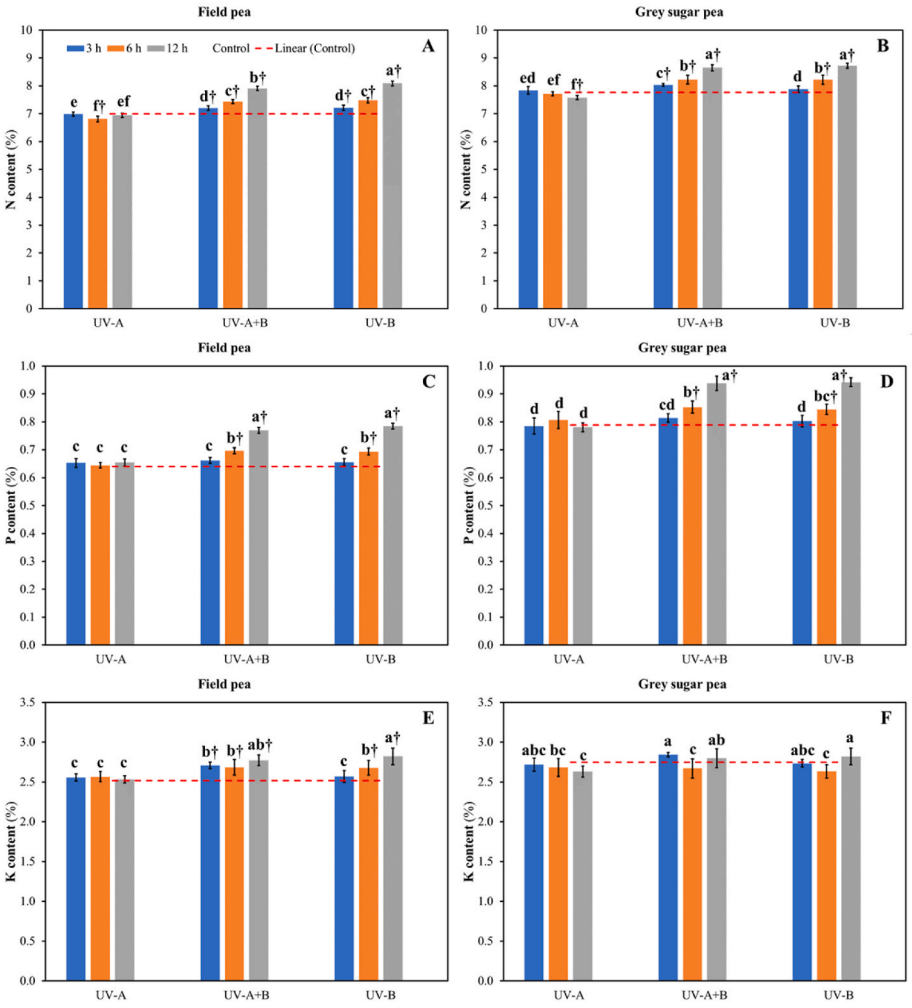

Fig. 4. Interaction effect of supplementary UV radiation and time of exposure on total nitrogen (A, B), phosphorous (C, D) and potassium content (E, F) of 'Field Pea' (A, C, E) and 'Dwarf Grey Sugar Pea' (B, D, F) shoots. Vertical bars indicate average values and standard error (n = 3). Different letters indicate significant differences at p = 0.05 according to the Tukey test. The dashed line indicates the average value of the control (greenhouse solar radiation). † indicates a significant difference compared to the control using contrasts in the linear mixed model.

3. Results

3.1. Effects on plant growth and yield components

UV treatment, time of exposure, and cultivar all had significant effects on the fresh weight of single pea shoots, fresh yield, dry biomass, and dry matter content (Table 1). There was a significant interaction between UV treatment and time of exposure for all yield components. Time of exposure and cultivar had significant interactive effects on fresh yield and dry matter content. There was also a significant interaction between UV treatment, time of exposure, and cultivar on single shoot fresh weight and dry biomass.

The interaction effect between UV treatment and time of exposure is presented in Fig. 3, showing that increased time of exposure only had significant effects on fresh yield for UVAB and UVB treatments. Compared to the untreated control, fresh yield decreased on average by 6.9 %, 14 %, and 35 % in 'Field Pea' and by 6.6 %, 16.2 % and 34.2 % in 'Dwarf Grey Sugar Pea' at 3, 6, and 12 h of UVAB and UVB exposure, respectively. This is with the exception of 'Dwarf Grey Sugar Pea', showing a 6.5 % increase in fresh yield at 12 h of UVA exposure compared to the control (Fig. 3B). A similar increase in plant biomass (9.3 %) can also be seen in dry weight for 12 h UVA treatment on 'Dwarf Grey Sugar Pea' (Fig. 3D). Dry matter content increased with increasing the time of exposure only in UVAB and UVB treatments. Compared to the untreated control, dry matter content increased by 8.8 % and 27.3 % in 'Field Pea' and 11.3 % and 25 % in 'Dwarf Grey Sugar Pea' with time of exposure of 6 and 12 h of UVAB and UVB radiation, respectively. 'Dwarf Grey Sugar Pea' had on average 13.5 % and 8 % higher dry weight and dry matter content, respectively, than 'Field Pea' across all treatments.

3.2. Effects on mineral content and accumulation

Supplemental radiation treatment, time of exposure, and cultivar significantly affected most mineral contents and mineral accumulation (Tables 2 and 3). There was a significant interaction effect between supplemental radiation and time of exposure on most minerals for both mineral content and mineral accumulation. Increasing the time of exposure, the content of N, P, Fe and Zn increased only in pea shoots exposed to UVB and UVAB radiation (Figs. 4 and 5). Compared to the untreated control, N content increased on average by 3 %, 6.6 %, and 14.2 % in 'Field Pea' and by 2.4 %, 5.9 % and 11.8 % in 'Dwarf Grey Sugar Pea' at 3, 6, and 12 h of UVAB and UVB exposure time, respectively. In the case of P content, an average increase of 8.6 % and 21.3 % in 'Field Pea' and by 7.7 % and 19.2 % in 'Dwarf Grey Sugar Pea' with time of exposure of 6 and 12 h to UVAB and UVB radiation, respectively. Compared to the control, increases up to 17.8 % and 20.9 % for Fe and 24.3 % and 25.5 % for Zn content were observed for 'Field Pea' and

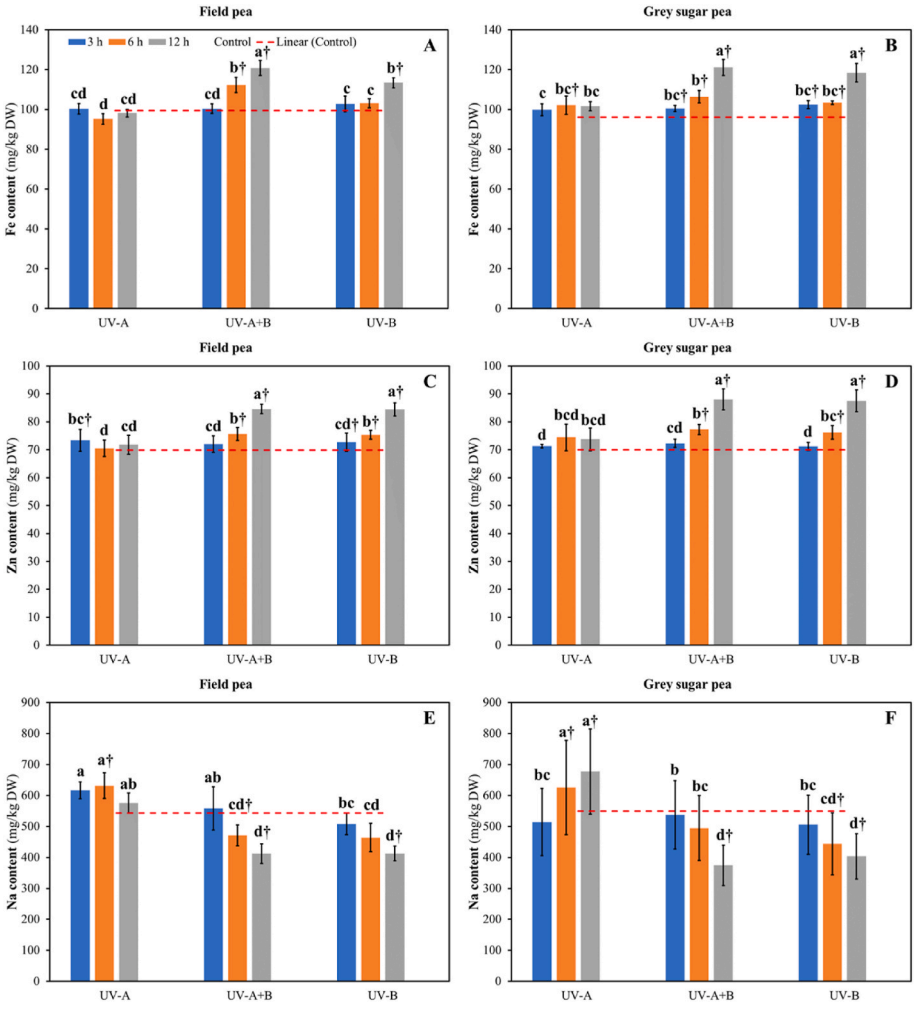

Fig. 5. Interaction effect of supplementary UV radiation and time of exposure on iron (A, B), zinc (C, D) and sodium content (E, F) of 'Field Pea' (A, C, E) and 'Dwarf Grey Sugar Pea' (B, D, F) shoots. Vertical bars indicate average values and standard error (n = 3). Different letters indicate significant differences at p = 0.05 according to the Tukey test. The dashed line indicates the average value of the control (greenhouse solar radiation). † indicates a significant difference compared to the control using contrasts in the linear mixed model.

'Dwarf Grey Sugar Pea', respectively, with time of exposure to UVAB and UVB of 12 h. The same effect, with an increase up to 14 % and 21.5 % compared to the control, was observed for the potassium content only in the case of 'Field Pea' exposed to UVB and UVAB radiation, respectively (Fig. 4E). An opposite effect was observed in the case of Na content, which decreased (up to 24.1 % and 29.3 % 'Field Pea' and 'Dwarf Grey Sugar Pea', respectively, compared to the control) with increasing the time of exposure only in peas exposed to supplemental UVB and UVAB radiation for both pea cultivars (Fig. 5E and F), while in the case of 'Dwarf Grey Sugar Pea' Na content increased up to 23.2 % with increasing the time of exposure to UVA (Fig. 5F).

Examining the mineral accumulation, the interaction effect between radiation treatment and time of exposure was opposite or not consistent with the effect observed for the mineral content and in some cases, the two pea cultivars showed a different response to radiation and time of exposure (Figs. 6 and 7). The accumulation of N and K decreased (on average up to 6.2 % and 14.3 %, respectively, compared to the control) with increasing the time of exposure to UVB and UVAB radiation while N and K increased (on average up to 8.1 % and 6.1 %, respectively, compared to the control) with increasing time of exposure to UVA radiation only in 'Dwarf Grey Sugar Pea' shoots (Fig. 6B and D), while limited effects were observed for the accumulation of the same minerals in the case of 'Field Pea' shoots (Fig. 6A and C). Similar trends were observed for Ca accumulation with average decreases up to 19.5 % and 13 %, compared to the control, in 'Field Pea' and 'Dwarf Grey Sugar Pea', respectively, with UVAB and UVB exposure of 12 h (Fig. 6E and F). The accumulation of Fe and Zn increased on average up to 17.1 % with the exposure to UVA radiation only in the case of 'Dwarf Grey Sugar Pea' (Fig. 7B and D). Instead, in the case of 'Field Pea', inconsistent or no effects were observed in terms of Fe and Zn accumulation (Fig. 7A and C). The accumulation of Na decreased (on average up to 35.1 % and 40.7 % compared to the control, in 'Field Pea' and 'Dwarf Grey Sugar Pea', respectively) with increasing the time of exposure to UVB and UVAB radiation in both cultivars, while it increased up to 36.2 % compared to the control with increasing the exposure to UVA only in the case of 'Dwarf Grey Sugar Pea' (Fig. 7E and F). With a few exceptions, the accumulation of most minerals was not different between plants exposed to supplementary radiation and those exposed only to solar radiation. There were no significant three-way interactions for mineral content or mineral accumulation. Comparing the two cultivars, 'Dwarf Grey Sugar Pea' had higher mineral content and accumulation than 'Field Pea' for all minerals except for Ca and Mg.

3.3. *Effects on chlorophyll and phytonutrients*

Supplemental radiation, time of exposure and cultivar had significant effects on chlorophyll *a*, chlorophyll *b*, chlorophyll *a*+b, total phenolics and total antioxidant activity except for any effect from

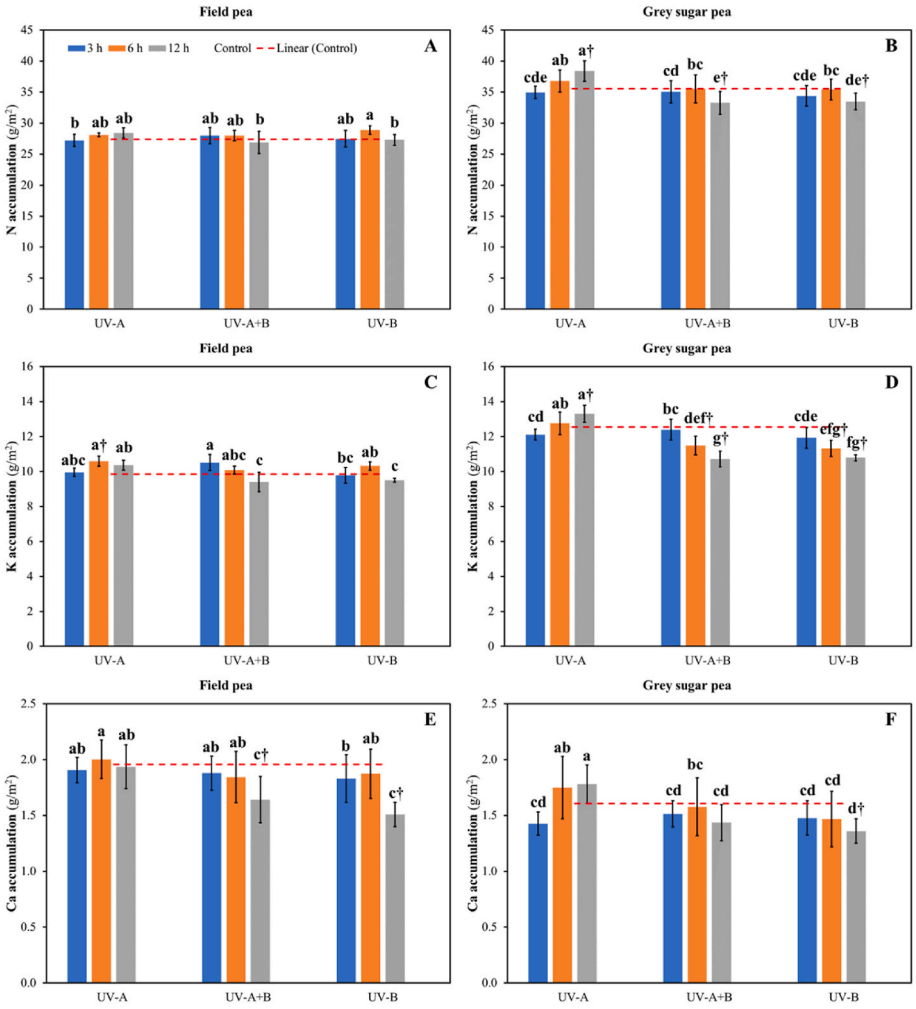

Fig. 6. Interaction effect of supplementary UV radiation and time of exposure on total nitrogen (A, B), potassium (C, D) and calcium accumulation (E, F) of 'Field Pea' (A, C, E) and 'Dwarf Grey Sugar Pea' (B, D, F) shoots. Vertical bars indicate average values and standard error (n = 3). Different letters indicate significant differences at p = 0.05 according to the Tukey test. The dashed line indicates the average value of the control (greenhouse solar radiation). † indicates a significant difference compared to the control using contrasts in the linear mixed model.

supplemental radiation on total antioxidant activity (Table 4). An interaction effect was observed between time of exposure and supplemental radiation on chlorophyll content and total phenolics (Fig. 8). Namely, that longer exposure times from both UVB and UVAB treatments on both cultivars resulted in decreased total chlorophyll (up to 24.3 % and 40.1 % compared to the control in 'Field Pea' and 'Dwarf Grey Sugar Pea', respectively) content and total phenolic content (up to 14.1 % and 18.8 % compared to the control in 'Field Pea' and 'Dwarf Grey Sugar Pea', respectively).

Regardless of the time of exposure, UVA supplemental radiation did not have a significant difference in any phytonutrients when compared to the control. Similarly, there was no significant difference between UVAB and UVB treatments. Supplemental UVB radiation significantly decreased all phytonutrients by an average of 12 % from the control. The largest decrease from supplemental UVB was chlorophyl b, being reduced by 22.8 % from the control. Additionally, 'Field Pea' had significantly higher chlorophyll content, total phenolic content, and total antioxidant activity than 'Dwarf Grey Sugar Pea' by 5 %, 13.5 %, and 16.9 %, respectively.

4. Discussion

The main objective of the study was to determine how supplemental UVA and UVB radiation, their combination, and the time of exposure affected the growth and nutritional profile of two cultivars of pea microgreens. Our results revealed a few interaction effects between UVA and UVB on pea microgreens, and relatively consistent effects of the time of exposure for both UVA and UVB radiation and their combination. The UVB and UVAB treatments were statistically not different for all dependent variables except for Fe and Zn content. Nevertheless, when considering the accumulation of minerals (estimated by multiplying the content of each mineral by the dry pea shoot biomass produced), no significant differences were observed between UVB and UVAB, also in the case of Fe and Zn. This leads to the conclusion that most changes were caused by UVB with no significant interaction effect between UVA and UVB radiation. These results suggest that UVA does not mitigate the negative impact of UVB radiation and are consistent with the hypothesis that plants respond to UVA and UVB radiation using different photoreceptors, which trigger multiple responses in terms of plant growth and physiology [12].

Iron and Zn content increased with UVB and UVAB radiation treatments compared to supplementary UVA radiation only and to the solar radiation control. Increased Fe content corroborates similar findings that UVB radiation increases free Fe content in plants at longer exposures due to its role in ROS (reactive oxygen species) counter-balancing [34] and could also be explained by the role Fe plays in regulating the stomata opening under UVB stress [35]. However, when considering the level of minerals accumulated UVB and UVAB supplementary radiation

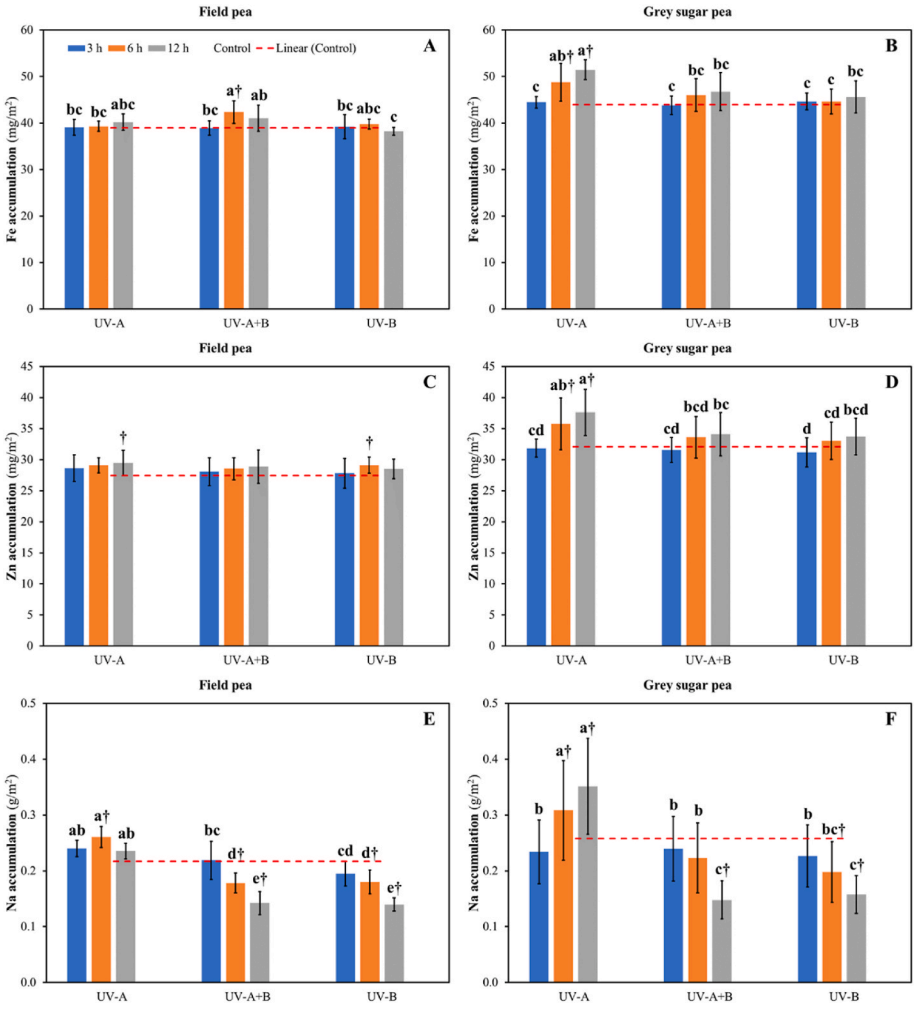

Fig. 7. Interaction effect of supplementary UV radiation and time of exposure on iron (A, B), zinc (C, D) and sodium accumulation (E, F) of 'Field Pea' (A, C, E) and 'Dwarf Grey Sugar Pea' (B, D, F) shoots. Vertical bars indicate average values and standard error (n = 3). Different letters indicate significant differences at p = 0.05 according to the Tukey test. The dashed line indicates the average value of the control (greenhouse solar radiation). † indicates a significant difference compared to the control using contrasts in the linear mixed model.

did not affect Fe and Zn compared to the application of UVA supplementary radiation and the solar radiation control. These results suggest that, when accounting for the overall plant dry biomass produced, the amount of Fe and Zn accumulated did not increase in response to supplementary UVB or UVAB radiation, and this effect may be largely due to the decrease of plant dry biomass observed with increasing exposure to supplementary UVB and UVAB radiation. The reduction of plant dry biomass typically observed under abiotic stress conditions, such as exposure to UVB radiation or salinity, may be caused by reduced photosynthesis and transpiration rates, with consequently reduced plant mineral uptake and accumulation [36–39]. Overall, the content of Fe and Zn observed in the present study were consistent or slightly higher compared to those observed in previous studies conducted on 'Dwarf Grey Sugar Pea' microgreens [22,23]. Considering that microgreens can be a good source of essential micronutrients like Fe and Zn [40,41], the results of the present study suggest that supplementary UVB and UVAB radiation may not negatively impact the accumulation of Fe and Zn in plants and thus their availability for our diet. Like in this study, Lee, Rivard, Pliakoni et al. [31] tested UVA, UVB, and UVAB treatments on lettuce and tomato. Their study also showed no significant difference between UVB and UVAB treatment effects on mineral content, apart from small differences in sulfur content in lettuce, and phosphorous content in tomatoes.

In general, UVA had much less of an effect than UVB on most variables. This is consistent with other studies showing that UVA does not cause any significant effect on shoot or root growth in many plants [42]. However, different species of plants react differently to UVA radiation, causing opposite reactions in many species [15]. Our results suggest that UVA has relatively little effect on pea shoot microgreen yield but does increase mineral content and accumulation in 'Dwarf Grey Sugar Pea'. In more detail, the effect of UVA supplementary radiation on fresh and dry biomass was influenced by the time of exposure, being tangible only in 'Dwarf Grey Sugar Pea' with a 12 h exposure. These results suggest that although minimal, the effect of UVA supplementary radiation is not detrimental, is genotype specific [43], and in selected genotypes, an exposure of at least 12 h of supplementary UVA radiation (1.83 W/m^2) can promote plant growth. The positive effect of UVA supplementary radiation on the mineral accumulation in 'Dwarf Grey Sugar Pea' was significant already with an exposure of 6 h/day, and may be explained by the positive effect on plant growth exerted by supplementary UVA radiation with longer exposure time, in this particular cultivar of pea microgreens. Enhanced plant growth, photosynthesis, and transpiration rates observed also in other studies [44,45], could explain the higher mineral accumulation observed in response to UVA radiation.

UVB radiation treatments caused slight decreases in mineral accumulation along with decreases in yield, which suggests that increased UVB radiation resulting from ozone depletion would lead to many

Table 4
Effect of UV supplementary radiation and time of exposure on the chlorophyll, total phenolics, and total antioxidant activity of 'Field Pea' and 'Dwarf Grey Sugar Pea' microgreens. [a].

	Chlorophyll *a*	Chlorophyll *b*	Chlorophyll *a*+b	Total phenolics	Total antioxidant activity
	mg/g DW			GAE mg/g DW	μM/g DW
Supplementary radiation (A)					
UVA	3.63 a	2.19 a	5.56 a	17.81 a	57.74
UVAB	3.35 b†	1.76 b†	4.86 b†	16.87 ab†	56.53†
UVB	3.33 b†	1.71 b†	4.80 b†	16.85 b†	55.86
Time of exposure (B)					
3 h	3.62 a	2.11 a	5.47 a	18.04 a	58.85 a
6 h	3.58 a	1.97 a	5.30 a	17.36 ab	59.25 a
12 h	3.10 b	1.57 b	4.45 b	16.13 b	52.03 b
Cultivar (C)					
'Field Pea'	3.50 a	1.96 a	5.20 a	18.27 a	61.14 a
'Dwarf Grey Sugar Pea'	3.38 b	1.81 b	4.95 b	16.09 b	52.28 b
A	***0.004***	***<0.0001***	***<0.0001***	***0.04***	*0.66*
B	***0.01***	***<0.0001***	***0.01***	***0.04***	***0.03***
A × B	***0.003***	***<0.0001***	***<0.0001***	***0.002***	*0.10*
C	***<0.0001***	***0.01***	***0.0001***	***<0.0001***	***<0.0001***
A × C	***<0.0001***	***0.03***	***0.002***	*0.47*	***0.03***
B × C	***<0.0001***	*0.14*	***0.002***	*0.12*	*0.11*
A × B × C	***0.005***	*0.73*	*0.36*	*0.16*	*0.40*
Control	3.66	2.28	5.68	18.07	61.44
Control vs UVA	*0.79*	*0.35*	*0.50*	*0.60*	*0.18*
Control vs UVAB	***0.02***	***<0.0001***	***<0.0001***	***0.02***	***0.05***
Control vs UVB	***0.02***	***<0.0001***	***0.0002***	***0.02***	*0.08*

[a] Reported values are averages of three growth cycles and replications. P-values are reported in italics for the main effects and their interaction, as well as for the contrasts between the control (solar radiation with no supplementary UV radiation) and different treatment groups. P-values ≤0.05 are reported in bold indicating a significant difference. The following symbol † indicates a significant difference compared to the control using contrast in the linear mixed model.

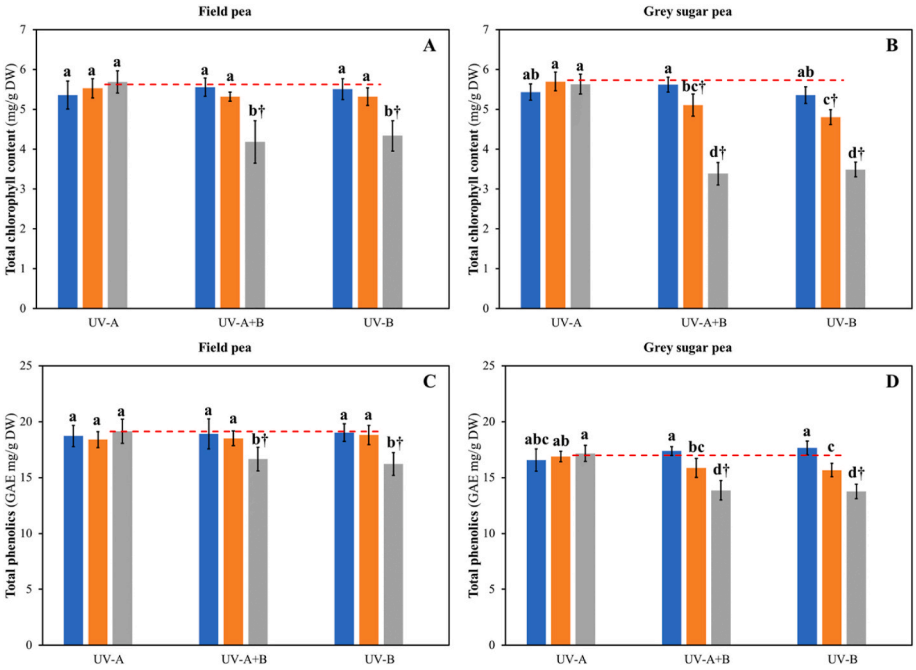

Fig. 8. Interaction effect of supplementary UV radiation and time of exposure on total chlorophyll (A, B) and total phenolic (C, D) content in 'Field Pea' (A, C) and 'Dwarf Grey Sugar Pea' (B, D) shoots. Vertical bars indicate average values and standard error (n = 3). Different letters indicate significant differences at p = 0.05 according to the Tukey test. The dashed line indicates the average value of the control (greenhouse solar radiation). † indicates a significant difference compared to the control using contrasts in the linear mixed model.

adverse effects on crops. Our results suggest that any increases in UVB radiation from ozone depletion (caused by any number of reasons), would likely cause large decreases in fresh weight and mineral yield among crops. Further, our results suggest that the intensity of UVB radiation used in this study (0.61 W/m^2), could cause a 10 % reduction in dry weight yield when administered for 12 h/day.

Other studies have shown that lower doses of UVB increase secondary metabolites due to the activation of UVB specific photoreceptors, which potentially can benefit human nutrition and plant defense [46]. However, our data show no change in phenolic compounds with 3 h/day exposures to UVB radiation in pea shoots. Notably, our data do show decreased phenolic content in pea shoots at longer UVB exposure times as other studies have also observed [47]. This is likely because at higher doses, UVB radiation degrades macromolecules and disrupts gene-transcription; therefore, this counteracts UVB photoreceptor pathways, resulting in decreased plant fitness and metabolite production

[46]. Nevertheless, it is worth noting that the content of total phenolics and total antioxidant activity observed in the present study were overall higher than those observed in previous studies conducted on 'Dwarf Grey Sugar Pea' microgreens [22,23].

Our results show that pea shoots treated with UVB for 12 h/day had significantly lower chlorophyll content than control and UVA treatments. This is consistent with other studies showing that UVB usually results in decreases of total chlorophyll content [15]. Decreased chlorophyll content is also likely caused by the degradation of macromolecules and metabolic pathways as described earlier by long durations of UVB radiation [46]. Chlorophyll content not only serves as a general proxy for the overall health of the plant but also contributes to the nutritional value of pea shoots [48]. There has been increasing evidence and studies on the health benefits of eating foods high in chlorophyll, meaning UVB exposure at long durations also decreases pea shoot nutrition in this way [49,50]. The statistically significant interaction we observed between the effects of UV treatment and cultivar suggests that 'Field Pea' is relatively more tolerant to UVB radiation damage than 'Dwarf Grey Sugar Pea'.

A recent study by Zhang et al. [51] using similar UVB irradiation and duration as this study, found that UVB increased phenolic content over short durations and antioxidant activity in both green- and red-leaf lettuce. Our results agree with theirs that long-term exposure to UVB decreases phenolic content. However, our results suggest that long-term exposure to UVB radiation decreases antioxidant activity whereas Zhang et al. found that UVB radiation increases antioxidant activity. These differences could be explained by different metabolic responses between lettuce and peas.

Another recent publication by Ali et al. [52] studying wild rocket (*Diplotaxis tenuifolia* (L.) DC.) shows how short term UVB irradiation (6 h of 4 W/m^2) causes increased amounts of secondary metabolites. Their findings have shown that longer term UVB irradiation causes overall decreased plant performance and chlorophyll content. Similarly, Dou et al. [53] found that basil (*Ocinum basilicum* L.) had increased phenolic content with short durations of UVB exposure, along with decreases in fresh weight. Ri et al [54] concluded in their long-term study over 30 days that UVB radiation was damaging at longer exposure time to the medicinal plant *Schisandra chinensis* (Turcz.) Baill., even at lower doses applied compared to our study (0.035 W/m^2).

5. Conclusions

Our study shows that there are few detectable compounding effects from UVA and UVB radiation when looking at nutritional profile of pea microgreens. Our data suggest that UVB has a more significant effect on the nutrition of pea microgreens than does UVA. Our research fits within the larger scholastic narrative that longer exposure times of UVB radiation adversely affects nutritional value and plant health. Although our data suggests that constant UVB radiation over just a weeklong period reduces antioxidant activity and overall mineral accumulation, small increases in mineral dry matter content were observed. Our literature review reveals that short duration bursts of UVB can help increase mineral content and antioxidant activity, which may be useful for indoor agriculture. However, at larger and longer scales of increased and uncontrolled atmospheric level, UVB radiation would be detrimental to overall crop health and nutritional value.

Future research is needed on the validation and understanding of what physiological processes are induced or altered in response to UVAB radiation. Likewise, while this study focused on pea microgreens grown over a period of 11 days, future studies involving full crop cycles will better inform long-term effects of UVAB radiation on crop health and nutrition.

CRediT authorship contribution statement

Daniel Winstead: Writing – review & editing, Writing – original draft. **Myungjin Lee:** Writing – review & editing, Methodology, Investigation, Formal analysis, Data curation. **Maria J. de Lima Brossi:** Writing – review & editing, Methodology, Formal analysis, Data curation. **Erin L. Connolly:** Writing – review & editing, Supervision, Resources, Funding acquisition. **Francesco Di Gioia:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

Declaration of competing interest

The authors declare no conflict of interest.

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Data availability

Data will be made available on request.

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