Title:

Effects of supplemental LED light quality and reduced growth temperature on swede (*Brassica napus* L. ssp. *rapifera* Metzg.) root vegetable development and contents of glucosinolates and sugars

Running title: Effects of LED light and reduced temperature on swede root vegetables

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Abstract

BACKGROUND: Low growth temperatures and the special light qualities of midnight sun in Northern Scandinavia, have both been shown to improve eating quality of swede root bulbs. To study the combined effect of these factors on root development and sensory-related compounds, plants were grown in phytotron under different 24 h supplemental LED light colours, at constant 15 °C, or reduced end-of-season temperature at 9 °C.

RESULTS: Far-red LED (730 nm) light induced longer leaves and produced more roundly shaped bulbs, than the other light quality treatments. At constant 15 °C, supplemental light of far-red LED also produced a stronger purple crown skin colour than the other LED treatments. This difference between light quality treatments disappeared at 9 °C, as all bulb crowns developed purple colour. There were no significant effects of LED-supplements on sugar concentrations, while the reduced temperature on average did increase concentrations of *D*-fructose and *D*-glucose. Total glucosinolate concentrations were not different among treatments, although the most abundant glucosinolate, progoitrin, on average was present in highest concentration under LEDs containing far-red light, and in lower concentration at 9 °C compared to 15 °C.

CONCLUSION: The light quality of 24 h photoperiods in combination with temperature appears primarily important for growth and morphological traits in swede root bulbs. Influence of light quality and low temperature on appearance and sensory-related compounds may be utilized in marketing of root vegetables with special quality related to growth conditions of high latitude origin.

Keywords: glucosinolates, light quality, morphology, temperature, swede, sugars

Introduction

Swede (or rutabaga) (*Brassica napus* L. ssp. *rapifera* Metzg.) is a root vegetable crop, mostly grown in northern regions of Europe and North America. In Northern Scandinavian countries, it comprises about 10% of the total vegetable consumption; being one of the few vegetables produced almost 100% domestically. It is commonly prepared freshly cut or cooked/mashed, and is important in the Scandinavian cuisine as an integral part of several festive dishes. With origins from Fennoscandia, swede roots were historically an important source of vitamin C and carbohydrates, predating potato as a key winter storage staple in the north (1). It also contains the secondary metabolite class glucosinolates (GLS), with potential dietary health benefits (2,3). The swede vegetable is an enlarged bulb of the stem base (hypocotyl) and upper part of the main root, developing in the first year of a biennial life cycle. Swede production is well suited for low temperatures, and root bulbs can be produced at average summer temperatures of 10-12 °C at Arctic latitudes in Scandinavia (4). These low growth temperatures seem to enhance especially sweet taste and other desirable sensory properties (5). Very long day lengths above the Arctic Circle also gives more rapid bulb growth than further south, which also contributes to an improved eating quality (4,6).

In general, plants sense diurnal changes in light and darkness by adjusting endogenous rhythms in response to inputs from blue light-receptors cryptochromes and zeitlupes, and red/far-red light detecting phytochromes (7). The summer season at latitudes above the Arctic Circle, however, has a 24 h photoperiod, with no distinct dark periods to reset internal clock factors to alternating light/dark cycles. At lower Arctic latitudes there are also prolonged periods with low solar elevation at night, where the solar spectrum is shifted towards red and far-red light (8). In addition, due to the low irradiance of low solar angles, the temperature at night can drop to around 5-6 °C. Furthermore, mean daily temperatures also drop in autumn above the Arctic Circle, due to the rapidly decreasing daytime solar elevations. This may especially be significant for phytochrome function in the north, as red:far-red perception is also dependent on the ambient temperature (9).

Soluble sugars are among the primary determinants for sweet taste in *Brassica* vegetables, and swede root bulbs normally contains more than fifty percent soluble sugars per dry matter (5). *D*-glucose, *D*-fructose and sucrose accumulates during the season in the growing tuber organ, as an energy store for later flowering/seed production (10). The concentration of sugars in swede also increases in response to lower air temperatures in autumn/winter, as seen in frost-free areas of Scotland, UK and southern Ontario, Canada (11, 12). The same is also true for cool growth temperatures, when tested under Arctic summer light conditions (5). Different day length conditions does not appear to influence sugar concentrations in swede at moderate temperatures close to 15 °C (6), although this has not been studied for lower temperatures.

GLS is a large family of defense-related sulphur containing glucoside-compounds, which are almost uniquely found within the *Brassicacae* order (13). Their breakdown products contribute to *Brassica* specific flavors, pungency and bitter taste. The aliphatic GLS sinigrin and progoitrinare extremely potent bitter agents (14), and progoitrin is one of the major glucosinolate types in swede (15). High ingestion of the metabolite goitrin can have negative (goitrogenic) effects on animal health (16). However, normal *Brassica* consumption by humans gives relatively low thiocyanate-doses, and reports of damages are extremely rare. Both light and temperature affect the accumulation of GLS in Brassicas (17). For swede, low growth temperatures under Arctic light conditions greatly reduces the progoitrin concentration, while warm growth temperatures elevates the concentration associated with a stronger bitter taste (5). In *Arabidopsis* there is diurnal upregulation of GLS biosynthesis in light (18), although the presence of 24 h midnight sun above the Arctic Circle on the other hand reduces progoitrin in swede root bulbs (6).

Northern light conditions above the Arctic Circle have on average 3-4 h longer daily photosynthetic light periods in summer than at lower latitudes in Fennoscandia, which in some varieties can compensate for sub-optimal temperatures (19). For swede, the presence of very long photosynthetic light periods gives a more rapid bulb growth compared to shorter day length conditions (6). In addition, in the presence of far-red rich solar irradiation at night there appears a reduction in GLS content of root bulbs. It is thus possible that diurnal spectral variation in the midnight sun period in combination with low growth temperature in late summer, affects GLS and the eating quality of swede at these latitudes.

The main aim of this study was therefore to investigate if there are effects of temperature and LED light qualities under very long photoperiods on growth, morphology and concentrations of GLS and sugars in swede, and secondly to see if there is an interaction between these two factors, under controlled conditions in phytotron.

Materials and methods

Plant materials and growth conditions

The experiment was performed in climate controlled growth chambers at the phytotron of the University of Tromsø. Swede seeds of the Norwegian cultivar 'Vigod' were sown in a moist mixture of standard fertilized peat soil (Floralux® Nittedal torvindustri, Arneberg, Norway) and perlite (70/30 volume) at 21 °C, and upon germination transferred to 15 °C and 24 h fluorescent growth light. Temperature was maintained constant at (±0.5 °C), and relative humidity adjusted to give a water vapour deficit of 0.5 kPa. Ninetysix seedlings were transplanted individually after 5 weeks each to a 7.5 liter pot containing new (70/30 volume,soil/perlite) growth substrate, with an addition of 9 g NPK mineral fertilizer (Fullgjødsel ® Yara Norge AS, Oslo, Norway) giving 1, 0.4 and 0.6 g NPK per plant, respectively. Boron was also supplied, with 0.1 g Borax (Searls Valley Minerals, Trona, California, US) per plant. During further growth, the plants were watered daily on-demand, and water content was controlled and adjusted weekly by weight.

After 6 weeks, all plants were transferred to dark chambers at 15 °C with 18 h daily photosynthetic active radiation, between 400-700 nm from fluorescent growth light (Phillips TLD 840, 150-200 µmol m^{-2} s^{-1}). Here, 16 plants per treatment were subjected to the following 24h supplement of different LED colours (Cluster LED 32, Flowmagic Agro LED, Kwintsheul, Netherlands) at a total 10 µmol m^{-2} s^{-1} irradiance for each LED-treatment (Table 1). Positive control treatment were included by 6 h day length extension control of fluorescent light bulbs (Energy Saver Osram DUlux 41-827 at 10-15 µmol m^{-2} s^{-1}), and negative control as 6 h darkness at night. Sixtyfive days after treatments started, eight plants within each treatment were transferred to identical light set ups at 9 °C. After a further 35 days, individual plants and root bulbs were measured and harvested in the morning and stored for 78 days in ventilated vegetable bags (polyethylene) at 0.5 °C. Then the individual roots were peeled, cut to approximately 1 cm cubes, thoroughly mixed and 100 g fresh mass cubes were rapidly frozen in liquid nitrogen and stored at -80 °C. All samples were weighed before lyophilization for 96 hours, and dry matter content was calculated based on difference between weight before and after. Dry sample cubes were ground to fine powder using porcelain mortar and pestle, and stored at -20 °C for 1-2 weeks until chemical analyses.

Soluble sugar contents

Freeze-dried samples of 50 mg were dissolved in 50 ml distilled water for one hour at room temperature, before centrifugation at 5’000 rpm for 10 min and transfer of clear supernatant to a new tube. Aliquots of 100µl were then analyzed for soluble sugars by enzymatic assay according the instructions of the Boehringer Mannheim Sucrose/D-Glucose/D-Fructose UV method (Cat.no. 10 716 260 035, R-Biopharm AG, Darmstadt, Germany). Concentrations were measured on a UV-visible light spectrophotometer at 340 nm (Smartspec Plus Spectrophotometer, Bio-Rad, Hercules, CA, USA).

Glucosinolate contents

Freeze-dried samples of 40 mg were pre-heated to 70 °C in 2.0 ml Eppendorf-tubes, before addition of 1.5 mL 70% methanol and 20 µL of Glucotropaeolin standard (50 µM, A AppliChem GmbH, Darmstadt, Germany). Tubes were immediately placed in a heating block at 70 ˚C for 30 min, and briefly mixed in a vortex mixer every fifth minute. Vegetable debris were centrifuged to the bottom at 13’000 rpm for 10 min at room temperature, and clear supernatant was transferred to a new tube and reduced to dryness in a Speed-Vac. The pellets were re-dissolved and vortexed in 500 µL MilliQ purified water, and passed through 0.45 µm centrifugal filters (VWR, Brooklyn, NY, US) by spinning briefly at 13’000 rpm at room temperature. The filtrate was transferred to HPLC sample vials. All samples were extracted and analyzed in randomized order by UPLC-HR-MS on a Waters Acquity UPLC (Milford, MA), coupled to Waters LCT-Premier time-of-flight MS with electrospray ionization. The extracts were separated on a Waters Acquity charged surface hybrid (CSH) C18 column (2.1 x 50 µm, 1.7 µm) using a gradient of 2-30% acetonitrile in water (both containing 0.1% formic acid) over 4 min at a flow rate of 0.6 ml/min. The injection volume was 1.00 µL, and the column temperature was kept at 40 °C. The glucosinolates were analyzed by negative electrospray ionization and m/z data from 150 to 1000 were acquired at a scan time of 0.25 s. Capillary and cone voltages were set at 2.4 kV and 50 V, respectively, while source and de-solvation temperatures were set to 120 and 300 °C, respectively. Nitrogen was used as de-solvation gas at 450 L/min. The MS was tuned to a resolution of 10,000 (FWHM) and leucine-enkephaline was infused through the reference probe for internal calibration during data acquisition. The peak for each glucosinolate (accurate mass ±0.05 Da) was integrated and the endogenous amounts were calculated based on the response of the internal standard.

Statistical analyses

All statistical analyses were performed using Minitab® version 16.1.0 (Minitab Inc., State College, PA, USA). Two-way ANOVA was used for analyses of effects of light quality and end-of-season temperature, with both factors defined as fixed variables. In addition, pairwise comparisons test were performed using Tukey with α set at 0.05.

Results

Effects of LED light and temperature on growth

Day length supplement with LED light had a significant effect on all measured growth parameters and yield (Table 2). The number of leaves (above 5 cm length), were lower under far-red LED light and in darkness control, compared to blue and red light. The number of leaves under R + FR and low irradiance supplement on the other hand were not different from red, far-red or darkness. Both treatments with FR light produced longer leaves than all the other treatments. The root bulbs also had lower root shape index (diameter/height) under both treatments FR light and R + FR light, and thus had a more round shape. All supplements with LED and low intensity fluorescent light produced a higher dry matter content of leaves than control treatment with darkness at night. The fresh weight of root bulbs reflected the leaf biomass, with lowest root fresh weight for the darkness control treatment. The dry matter content in bulbs was generally lower in LED light containing far-red and in the dark control, compared to the other light treatments, and lower at 15 °C end of season temperature.

The treatments with reduced temperature 9 °C during the period of root bulb growth, also resulted in significantly lower number of leaves and lower dry matter leaf biomass than at constant 15 °C (Table 2). The root bulb fresh mass was thus also lower for the treatments at 9 °C, compared to 15 °C. There was no significant interaction between temperature and light treatments for plant growth parameters, except for dry matter content of root bulbs and a weak interaction for leaf length. However, there were no significant differences in leaf length between all treatments, nor for dry matter content between the LED treatments. The skin colour of the crown was dark purple in all roots grown at 9 °C, and in the roots with supplement of far-red, low irradiance fluorescent and darkness at constant 15 °C. Root bulbs from the other LED treatments at 15 °C were light purple in the crown (Figure 1).

Effect of light quality and temperature on glucosinolates in peeled roots

Eleven glucosinolates were detected in the root bulb flesh, including six aliphatic, four indolic and one aromatic glucosinolate. The aliphatic glucosinolates were in decreasing order of concentrations: progoitrin (PRO), glucoberteroin (GBT), glucoerucin (GER), gluconapoleiferin (GNP), glucoalyssin (GAL) and glucoraphanin, which alltogether comprised 84-86% of the total glucosinolate content. The concentration of indolic glucosinolates were in decreasing order glucobrassicin (GBR), neo-glucobrassicin (neo-GBR), 4-methoxy-glucobrassicin and 4-hydroxy-glucobrassicin. The total content of indolic GLS was similar to the content of the aromatic gluconasturtin (7-8% of the total content). Some glucosinolates in concentrations below 0.2 µmol/g DM were not detected in all samples. Only GLS types above this concentration were analysed statistically for influence of light quality and temperature (Table 3). There was a significant effect of light quality supplement for five of the detected glucosinolates. On average (across two temperatures), progoitrin were in lowest concentration under day length extension with fluorescent white light, which also was the case for glucoerucin and glucobrassicin. Progoitrin were detected in highest concentration under far-red light and glucoerucin under red light. Gluconapoleiferin and the indolic glucobrassicin, neo-glucobrassicin and 4-methoxy-glucobrassicin were detected on average in highest concentration with no day light extension. Total indolic GLS were therefore highest when there was a distinct 6 h dark period as part of the photoperiod. Total aliphatic GLS were not significantly influenced by LED light qualities nor the photoperiod.

On average (across light qualities), low temperature of 9 °C during the development of the root bulb resulted in lower concentration of progoitrin and 4-methoxy-glucobrassicin and higher concentration of glucoallysin and glucobrassicin, compared to 15 °C. However, the total content of glucosinolates were not affected significantly by the reduced temperature. Temperature interacted with light quality for only glucobrassicin, resulting in higher concentration in red light at reduced 9 °C temperature compared to constant 15 °C.

Effect of light quality and temperature on sugars in peeled roots

There were no significant differences between the different light treatments for concentrations of sucrose, *D*-glucose and *D*-fructose. However, there was a strong effect of temperature during root bulb development, with significantly higher concentrations of *D*-glucose and *D*-fructose in root bulbs at 9 °C compared to at 15 °C (Figure 2). There was no significant interaction between light and temperature treatments for sugar content.

Discussion

The results of the current study demonstrate an effect of both temperature and light quality of 24h photoperiods on growth and morphology of swede roots. The main effect of reduced temperature during bulb development was a reduction of growth rate, as previously seen in phytotron-experiments under natural light (5). For the effects of light quality, the unique influence of LED treatments containing far-red in causing longer leaves and more roundly shaped root bulbs, strongly suggest an involvement of phytochrome(s) with an excessive elongation similar to low R:FR shade-avoidance responses (20). The wavelength maximum of the used far-red LED at 730 nm, also fits well with observed maximum absorption- and action-spectra of phytochrome P_{fr}-isomers (21,22). A similar experimental set-up using the same LEDs for broccoli, also resulted in longer plant height under far-red light (23). The presence of far-red light or darkness may also be important for the intensity of violet crown colour in swede, as these treatments appeared to counteract the previously observed effect of warm growth temperature reducing the intensity of violet crown colour (5). It is, however, difficult to distinguish if our observed far-red effects are attributable to shade-avoidance/end-of-day far-red or a photoperiodic response, although far-red results grouping together with 6 h darkness control for some responses may support the former. On the other hand, for broccoli there are no similarities between a 12 h darkness and supplemental far-red LED in growth responses, indicating a photoperiodic response to far-red light (23).

The observation of some specific GLS types at highest concentration in 6 h darkness at night, and lowest concentration in 24 h white light, largely agrees with results of a previous phytotron study of swede under 24 h natural light at 69.7°N 18.9°E (6). Similar effects of 24 h versus 12 h photoperiod was also observed for GLS accumulation in curly kale and broccoli (23, 24). This does suggest that diurnal light/dark cycling is positive for GLS accumulation in *Brassica*, as opposed to in photoperiods of 24 h light at high latitudes. This is unexpected, considering that light is indeed positive for progoitrin concentrations in swede seedlings (25).

The influence of LED colours used in the current study were small for GLS, except for higher levels of progoitrin under far-red suplemental light. This is in contrast to broccoli florets, which has lowest total GLS contents under far-red LEDs (23). In field trials of turnip, including reflective coloured mulches and different coloured nets above plants, there was on the other handlittle influence of light quality on GLS in root bulbs and greens (26, 27). It is thus difficult to conclude how light qualities may affects GLS across *Brassica* species and cultivars, and within different plant parts.

The observation of larger concentration of sugars at low versus high end-of-season temperature, confirms the findings of several studies of swede root bulbs. Another study of the same cultivar under 24 h natural light (69.7°N 18.9°E), also revealed a negative relation for sugar concentrations over a larger temperature range from 6 °C to 21 °C than in the current study (5). High sugar levels has also been observed at low temperatures in several field studies at contrasting day length conditions in winter at southern latitudes, and at northern versus southern latitudes in summer in Scandinavia (4, 28, 29). The latter also included a comparison entailing longer day lengths for the northern sites, but the results of the current study and previous comparisons of different day lengths in phytotron (69.7°N 18.9°E) do not show any effect of light conditions on sugars in swede (6). In broccoli however, there is an interaction between warm temperature and far-red LED light in 24 h day length, elevating concentrations of D-fructose compare to a lower temperature (23). In seedlings of *Brassica*, the composition of soluble sugars varies greatly across species under different supplemental LED light colours (30). This illustrates the need for more trials of other crucifer species and varieties under different light and temperature regimes. It is also worthwhile to consider if relatively small changes in sugar levels may still have an influence on sensory quality, as perception of sweet/bitter taste in *Brassicas* is co-dependent on concentrations of bitter GLS types (31). The observed increase of progoitrin under far-red light could therefore have implications for sweet/bitter taste in swede root bulbs, although the maximum concentration difference of 0.8 µmol g^{-1} between light qualities is rather modest compared to the 8.6 µmol g^{-1} difference between temperatures ranging from 9 to 21 °C (5).

In conclusion, the light quality of 24 h photoperiods appears to be important for growth and morphological traits in swede, and may influence some sensory related GLS. Furthermore, the presence of end-of-season low temperatures can increase sugar levels and reduce the bitter progoitrin, which may be used in marketing of swede products from Arctic growth conditions with special appearance and sensory quality.

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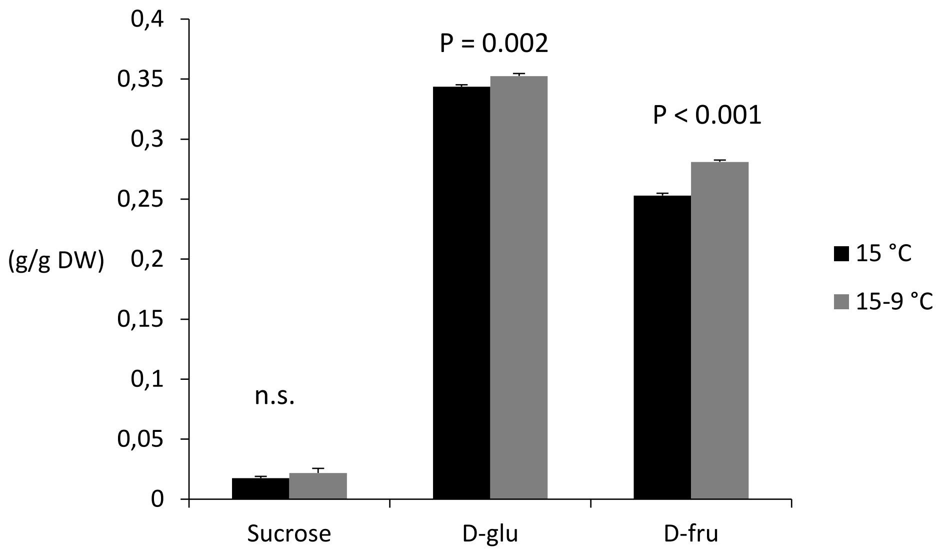
Figure legends

Figure 1. Crown skin colour development of Swede roots grown under 24 h photoperiod with (A) supplement red LED at constant 15 °C and (B) supplement far-red LED at reduced end-of-season temperature 9 °C (last 35 days).

Figure 2. Concentrations of soluble sugars in peeled swede root bulbs at different temperature regimes during bulb development. Average results across six light treatments (n= 26) with standard error mean indicated with bars, and statistical difference with corresponding p-values.


A
B



0,4
0,35
0,3
0,25
0,2
0,15
0,1
0,05
0
(g/g DW)
P = 0.002
P < 0.001
n.s.
Sucrose
D-glu
D-fru
15 °C
15-9 °C

Figure 2.

Table 1. Experimental end-of-season temperature and light quality as supplement to 18 h daily photosynthetic fluorescent light, including: coloured light emitting diodes (LED), low irradiance (l.i.) fluorescent light or darkness at night.

No.	Light quality (duration)	Temperature (period)
1.	Red LED (24 h)	15°C (100 days)
2.	Far-red LED (24 h)	15°C (100 days)
3.	Red:far-red LED (1:1) (24 h)	15°C (100 days)
4.	Blue LED (24 h)	15°C (100 days)
5.	l.i. fluorescent (6h night)	15°C (100 days)
6.	Darkness (6h night)	15°C (100 days)
7.	Red LED (24 h)	15°C (65 days) – 9 °C (35 days)
8.	Far-red LED (24 h)	15°C (65 days) – 9 °C (35 days)
9.	Red:far-red LED (1:1) (24 h)	15°C (65 days) – 9 °C (35 days)
10.	Blue LED (24 h)	15°C (65 days) – 9 °C (35 days)
11.	l.i. fluorescent (6h night)	15°C (65 days) – 9 °C (35 days)
12.	Darkness (6h night)	15°C (65 days) – 9 °C (35 days)

Table 2. Effects of light quality and temperature on growth and development of swede plants (*Brassica napus* L. ssp. *rapifera* Metzg.) and root bulbs. Growth conditions included 18 h daily fluorescent growth light for all plants, with either 24h LED supplement of red(R), far-red(FR), blue(B), supplement of 6h low intensity fluorescent light or 6 h darkness at night. These were given in combination with temperature regimes of either constant 15 °C (100 d) or 15 °C (65 d) followed by 9 °C (66 -100 d). Significant difference (Tukey, p≤0.05) within columns are indicated with different letters, and corresponding GLM-ANOVA p-values. Sample size n = 7-8 individual roots per treatment.

Treatment	No. of leaves	Leaf length (cm)	Leaf DM (g)	Root FM (g)	Root DM (%)	Root shape index[†]
15°C						
24h LED R	12.0 ab	40.1 c	14.6 ab	802 ab	12.0 bc	1.80 a
24h LED FR	10.8 abcde	47.8 ab	13.5 abc	814 a	11.0 cd	1.63 bcd
24h LED R+FR	10.9 abcd	49.4 a	14.8 a	790 abc	11.7 bcd	1.62 cd
24h LED B	12.3 a	38.7 c	14.7 a	816 a	11.8 bcd	1.77 ab
6h l.i. fluorescent	11.3 abc	39.3 c	14.7 a	770 abcd	11.5 bcd	1.76 abc
6h darkness (control)	11.1 abcd	39.1 c	12.1 bcd	652 ef	10.9 d	1.70 abcd
15°C-9°C						
24h LED R	10.0 bcdef	37.2 c	12.6 abcd	702 cdef	12.4 b	1.73 abc
24h LED FR	8.5 f	51.8 a	12.1 bcd	778 abc	11.9 bcd	1.62 cd
24h LED R+FR	8.8 ef	49.6 a	11.7 cd	708 bcdef	11.5 bcd	1.57 d
24h LED B	9.9 cdef	41.4 c	12.0 cd	740 abcde	12.6 b	1.73 abc
6h l.i. fluorescent	9.1 def	36.9 c	11.4 cd	675 def	13.8 a	1.70 abcd
6h darkness (control)	8.4 f	43.0 bc	10.0 d	626 f	12.3 b	1.73 abc
p-values						
Light quality (L)	0.001	<0.001	<0.001	<0.001	<0.001	<0.001
Temperature (T)	<0.001	n.s.	<0.001	<0.001	<0.001	0.075
L x T	n.s.	0.016	n.s.	n.s.	<0.001	n.s.

[†]Root diameter/root height

Table 3. Effects of light quality (L) and temperature (T) on glucosinolate (GLS) concentrations (µmol g^{-1} DM) in peeled root bulbs of swede. Light quality treatments included: 24h LED supplement of red (R), far-red (FR) and blue (B), 6h day length extension with low irradiance white (W) fluorescent light or 6h darkness (D) at night. Temperature treatments were constant 15 °C for 100 days or 15 °C for 65 days followed by reduced 9 °C for 35 days. Significant difference (Tukey, p≤0.05) within columns are indicated with different letters, and corresponding GLM-ANOVA p-values. Sample size n = 7-8 individual roots per treatment.

Treatment	GER[†]	PRO	GBT	GAL	GNP	GNS	GBR	NGB	Alifatic GLS	Indolic GLS	Total GLS
15°C											
24h LED R	1.09	4.09 ab	2.89	0.60	0.92	0.91	0.23 c	0.30 abc	9.87	0.62 b	11.40
24h LED FR	1.03	4.44 a	2.87	0.61	0.78	0.90	0.26 abc	0.28 bc	10.07	0.62 b	11.60
24h LED R+FR	0.95	4.24 ab	2.77	0.66	0.85	0.83	0.24 c	0.33 abc	9.78	0.66 b	11.27
24h LED B	1.05	3.56 ab	2.75	0.59	0.85	0.84	0.26 abc	0.33 abc	9.07	0.68 b	10.59
6h W	0.89	3.54 ab	2.52	0.64	0.96	0.75	0.22 c	047 ab	8.79	0.80 ab	10.34
6h D	0.98	3.64 ab	2.79	0.61	0.95	0.78	0.40 ab	0.50 a	9.55	1.05 a	11.44
15°C-9°C											
24h LED R	1.09	3.29 ab	2.81	0.73	0.94	0.98	0.40 a	0.40 abc	9.23	0.89 ab	11.1
24h LED FR	0.96	3.78 ab	2.49	0.67	0.71	0.98	0.34 abc	0.27 c	8.97	0.69 b	10.64
24h LED R+FR	1.12	3.92 ab	2.91	0.80	0.77	0.96	0.31 abc	0.29 bc	10.08	0.70 b	11.75
24h LED B	1.00	3.29 ab	2.49	0.70	0.77	0.76	0.33 abc	0.36 abc	8.60	0.78 ab	10.13

6h W	0.88	2.95 b	2.34	0.68	0.77	0.80	0.30 abc	0.40 abc	8.01	0.77 ab	9.58
6h D	1.09	3.76 ab	2.69	0.74	0.96	0.89	0.34 abc	0.39 abc	9.54	0.82 ab	11.25
p-values											
Light quality (L)	0.045	0.023	n.s.	n.s.	0.020	n.s.	0.029	<0.001	n.s.	<0.001	n.s.
Temperature (T)	n.s.	0.015	n.s.	<0.001	n.s.	n.s.	<0.001	n.s.	n.s.	n.s.	n.s
L x T	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	0.037	n.s.	n.s.	0.008	n.s

[†]Glucoerucin (GER), progoitrin (PRO), glucoberteroin (GBT), glucoallysin (GAL), gluconapoleiferin (GNP), gluconasturtiin (GNS), glucobrassicin (GBR), neo-glucobrassin (NGB)