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Sprout Growth Inhibition and Photomorphogenic Development of Potato Seed Tubers (*Solanum tuberosum* L.) Under Different LED Light Colours

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Abstract

Green-sprouting potato seed tubers in light and elevated temperatures are vital for production in short-season climates. Using light-emitting diodes (LEDs) to inhibit sprout elongation during pre-sprouting may represent an energy-efficient alternative to traditional indoor light sources. Sprout growth inhibition and some photomorphogenic responses were therefore examined in potato cultivars exposed to LEDs of different wavelength maxima and irradiance rates. Red LED (660 nm) produced the strongest inhibition of sprout elongation at very low irradiances 10–100 nmol m^{-2} s^{-1}, while far-red LED (735 nm) produced the strongest inhibition at higher irradiances. This inhibitory pattern was similar in all cultivars, although the degree of inhibition varied. The colour of sprouts and tuber skin remained etiolated under far-red LED, in contrast to LEDs between 380 and 660 nm which developed green colour intensity in an irradiance-dependent manner. Mixtures of red and far-red light, and pulses including red/far-red reversals did not produce stronger inhibition, except in some instances where total fluence was increased. Furthermore, green-sprouting under different LED colours did not seem to affect subsequent emergence and growth after planting. The current results suggest an involvement of multiple phytochromes in de-etiolation and sprout growth inhibition in seed potato tubers, which may be selectively utilised in LED-based green-sprouting in red and far-red wavelengths.

Keywords De-etiolation · Far-red light · Green-sprouting · Photomorphogenesis · Phytochrome · Red light · Sprout elongation

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List of Abbreviations

B	Blue
DAP	Days after planting
FR	Far-red
G	Green
HIR	High irradiance response
LED	Light-emitting diode
R	Red
VLFR	Very low fluence response
UV-A	Ultraviolet A

Introduction

Pre-sprouting seed potatoes in natural or artificial light, also referred to as green-sprouting or chitting, is an effective method to advance emergence and shorten the growth cycle (McKeown 1994). This practice is vital for potato production at sites restricted by short growing seasons, especially at high northern latitudes (Furunes 1990; Knowles and Botar 1992; Essah and Honeycutt 2004; Eremeev et al. 2008). Green-sprouting can also be used for gaining earlier market access, manipulating tuber/crop size and avoiding late-season occurring diseases, such as late blight (Möller 2007; Hagman 2012). Furthermore, in tropical regions with limited possibilities for cold storage, diffused daylight is sometimes used to limit sprout growth during long-term storage of seed tubers for the next season (Potts 1983). Sprouting and accelerated physiological development in the seed potato is primarily driven by exposure to elevated temperature (above 4 °C) (Blauer et al. 2013; Sonnewald and Sonnewald 2014), but the combination with light is necessary to avoid elongated and weakly attached sprouts. Short robust sprouts are especially important for mechanised planting, as unwanted abscission of sprouts will delay field emergence and can reduce the yield potential (Allen 1978; McGee et al. 1988b). The use of light from light-emitting diode (LED) systems may provide a more energy-efficient light source in green-sprouting seed tubers than traditional light sources at high latitudes. Application of selective wavelengths may also open for new technological developments, as exemplified by blue LEDs promoting growth potential, photomorphogenesis and subsequent survival after cryopreservation of potato clones (Edesi et al. 2017).

Plant development in darkness (skotomorphogenesis) is characterised by pale etiolated tissues, excessive shoot elongation, poor leaf development and an apical hook, as an adaptation to penetrate soil and litter to reach the light (Godlewski 1889; Darwin 1896). This developmental state in seedlings is due to a default repression of photomorphogenesis. Illumination with low intensities of light removes this inhibition and triggers a shift in gene-expression towards development in light and photosynthesis (Dong et al. 2015). This implies an opening of the apical hook, reduced elongation growth, leaf expansion and chloroplast development. The initial stage of de-etiolation is a very low fluence response (VLFR), where highly abundant phytochrome A detects very low irradiances of far-red light and which upon activation is rapidly degraded (Casal et al. 2014). Under a dense leaf canopy rich in far-red light, this can

proceed as a saturating high irradiance response (HIR) through phytochrome A. Alternatively, in direct sunlight, it may proceed as a low fluence HIR through cryptochrome and the photo-reversible/"light stable" phytochrome B, responding to wavelengths from blue to far-red light (Casal et al. 2014). However, in spite of the well-known propensity of phytochrome A for degrading in light, it can also display some photo-reversibility between red-absorbing and far-red-absorbing isoforms at very short light exposures of less than a minute (Shinomura et al. 2000).

The morphogenetic distinction between development in darkness and light also holds true for sprouting potato tuber buds (Dinkel 1963; Goodwin 1967), although the underlying regulatory mechanism has yet to be characterised at the molecular level. Sprout elongation rates in tubers are greatly reduced upon transfer from darkness to light and, vice versa, elongation rates increase rapidly upon transfer from light to darkness (McGee et al. 1987a). This inhibition of elongation appears to be more dependent on total incident energy, rather than the daily duration of illumination, thus resembling HIRs as described for seedlings in other species. By using narrow wavelength-specific filters, it has also been shown that wavelengths of especially red/far-red light around 700 nm and blue light between 400 and 500 nm are most effective in inhibiting elongation in potato sprouts, with high degrees of inhibition at irradiance rates as low as 10–20 nmol m^{-2} s^{-1} (McGee et al. 1987b).

In Northern Scandinavian potato production, it is common practice to expose tubers to temperatures around 10–12 °C and light, during a 6–8-week pre-sprouting period before planting. Light sources for this are usually solar radiation or fluorescent or incandescent light sources indoors. Green-sprouting tubers outside at ambient temperatures, however, carry some risks of frosts in early spring. Maintaining temperatures in indoor storage chambers may also be challenging in late spring due to heat dissipation from light sources, which may require cooling of the rooms to avoid excessive physiological ageing. The use of LED lights during green-sprouting can therefore represent an advantage to farmers in these areas, by preventing excessive heat build-up and reducing energy costs (Morrow 2008). In addition, a more sophisticated approach by mixing of different LED colours and intensities may further enhance the advantages of LED light application in green-sprouting by selective induction of multiple photo-receptor systems (Mitchell 2015). Cryptochromes and different phytochromes are here prime candidates as photo-receptors for growth inhibition in green-sprouting tubers at blue and far-red wavelengths.

There are currently no reported studies, where LED lights of different wavelength maxima and intensities have been used for green-sprouting of potato seed tubers, and no studies on the combination of different wavelengths. Our main aim was therefore to study if LED light(s) of selective wavelengths may be used to inhibit sprout growth during pre-sprouting of Norwegian potato cultivars. We did this by the following objectives: (1) to identify the most effective LED wavelengths and their fluence-dependence on inhibiting sprout growth and inducing de-etiolation of seed tubers, (2) to find the effect of mixing the most effective LEDs for these responses, and (3) to explore for possible influence of different LED colours on subsequent growth vigour.

Materials and Methods

Plant Material

Post-dormant potato seed tubers were used in all LED exposure experiments from January to July in 2016 and from February to April in 2017. The cultivars were Asterix (medium late, consumption and processing), Folva (medium early, consumption and processing), Mandel (late, consumption) and Gullauge (medium late, consumption). On-location produced seed tubers of Asterix were used in the first experiment in 2016. All subsequent experiments used pre-basic seed tubers of Asterix, Folva and Mandel (Overhalla Klonavlssenter, Norway) and basic seed tubers of Gullauge.

Light Sources Used in the Experimental Conditions

The LED treatments in all experiments were carried out in climate-controlled dark chambers at Biologisk klimalaboratorium Holt, University of Tromsø. Temperature was set at 15 °C (± 0.5 °C), and humidity was adjusted to a water vapour pressure deficit of 0.5 kPa, which is sufficiently low to prevent root growth during sprouting (Johansen and Mølmann 2018). Exposure to LEDs of different wavelength maxima was supplied by programmable growth light RX-30 units (Heliospectra AB, Gothenburg, Sweden) (Fig. 1). The RX-30 units were suspended at the top of enclosed trolleys (0.5 m × 0.5 m), with a black tightly woven plant cover around all sides. The output radiant flux of the LEDs in RX-30 units can be programmed with linear intensity levels between 0 and 1000, and up to 150 timed changes per 24 h. The irradiance at the tuber level in experimental treatments was measured using a Jaz Spectral Sensing Suite (Ocean Optics, Dunedin, FL, USA). The irradiances of individual LED exposure treatments were set up by changing the intensity settings of the RX-30 units and adjusting the distance of the trolley's shelf from the RX-30 units between 78 and 148 cm. Fluorescent white light at 2.8–4.6 μmol m^{-2} s^{-1} (OSRAM, DULUX EL LONGLIFE, 20W/41-827, made in Germany) was used as a positive control, and complete darkness was used as a negative control, by covering with double layers of black cotton fabric. The irradiance of the fluorescent white light was within the lower range of indoor light levels commonly used for green-sprouting in Norway.

Experimental Pre-treatments, Handling and Observations of Tubers

Prior to LED exposures, tubers were taken from storage (3.5 °C) and pre-sprouted in darkness at 15 °C for 5–10 days, resulting in 1–2-mm sprouts at the onset of experimental treatments. The pre-sprouted tubers were randomly picked in darkness and distributed evenly on the bottom of transparent polystyrene boxes without lids (19 cm × 26 cm × 7 cm), which were subsequently placed in different light exposure treatments (Table 1). The open boxes were placed either centrally for experiments with one cultivar or bisymmetrically around the center of the 0.5 m × 0.5 m shelf in the trolley, when four cultivars were tested. The longest sprout on each tuber was measured at the end of the LED treatment period. Occasionally, subapical necrotic lesions occurred on sprouts in some cultivars, likely due to Ca-deficiency in elongating sprout tips (Tzeng et al. 1986). This was most prevalent in dark control treatments, which had the longest

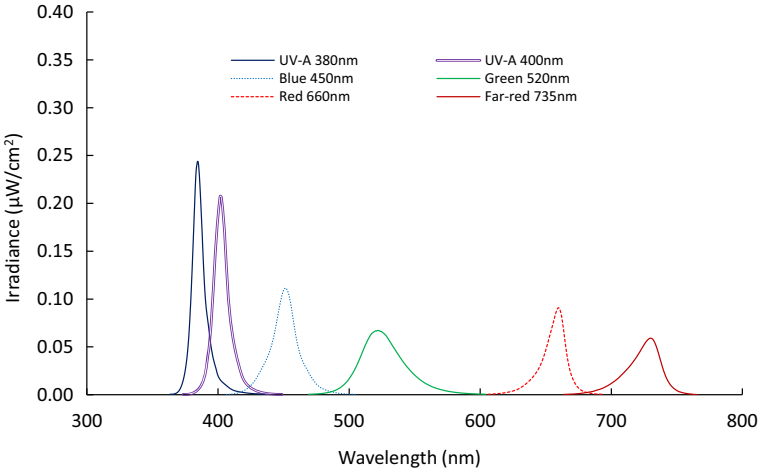

Fig. 1 Spectral distribution of light-emitting diodes with different wavelength maxima (RX-30, Heliospectra AB, Sweden) used in the experiments

sprouts. For practical reasons, and to avoid risks of accidentally triggering very low fluence light responses, we decided not to alleviate this by spraying calcium sulfate solution on sprouts during treatments. Tubers with visible necrotic lesions were not included in the analyses. After treatments, the resultant colouration of sprouts and potato skin was assessed visually in all tubers by comparing all treatments side by side, within each cultivar.

Experimental LED Setup and Trials

The series of LED experiments were conducted from January 2016 to April 2017 with different light quality treatments and irradiances (Table 1), for optimal utilisation of available RX-30 LED units. LED exposures were given for 21 days, except for experiment (exp.) 1 in 2016 with 23 days, and 14 days in exp. 6 in 2017.

Photomorphogenic Development and Sprout Growth Under LED Lights

Exp. 1 was performed on January 2016 with pre-washed Asterix to test the effects of LEDs with maxima of blue (B), red (R) and far-red (FR) light (at 90 nmol m^{-2} s^{-1}) on de-etiolation including greening of sprouts and tuber skin and inhibition of sprout elongation. This experiment also included a test of different red irradiance levels from 10 to 900 nmol m^{-2} s^{-1}. Ten tubers were measured/observed per light quality treatment or irradiance.

Fluence Dependency of Sprout Growth Inhibition Under LED Light

In exp. 2 and 3, we included all four cultivars and tested blue, red and far-red LED at contrasting very low 10 nmol m^{-2} s^{-1} and high irradiance 1000 nmol m^{-2} s^{-1}, in order to determine if the suppression of sprout growth was fluence-dependent and if this

Table 1 Overview of experiments with light quality treatments and various irradiances, involving LEDs with wavelength maxima in UV-A (380 or 400 nm), blue (B, 450 nm), green (G, 520 nm), red (R, 660 nm) and far-red (FR, 735 nm) light. White fluorescent light (W) and darkness (D) were used as controls

	Date	Time (days)	Light quality and irradiance (nmol m^{-2} s^{-1})	Cultivars	Tubers per treatment (*n*)
Exp. 1 (2016)	27 Jan–19 Feb	23	B (90) R (10, 30, 90 and 900) FR (90) W (4600) D (0)	Asterix	10
Exp. 2 (2016)	17 Mar–7 Apr	21	B (10 and 1000) R (10 and 1000) FR (10 and 1000) W (2800) D (0)	Asterix, Folva, Mandel, Gullauge	12
Exp. 3 (2016)	21 Apr–12 May	21	B (10 and 1000) R (10 and 1000) FR (10 and 1000) W (2800) D (0)	Asterix, Folva, Mandel, Gullauge	12
Exp. 4 (2016)	18 May–8 Jun	21	UV-A 400 nm (100) B (100) G (100) R (100) FR (100) W (2800) D (0)	Asterix, Folva, Mandel, Gullauge	12
Exp. 5 (2016)	14 Jun–5 Jul	21	R (10) FR (10) R:FR mix (20) W (2800) D (0)	Asterix, Folva, Mandel, Gullauge	12
Exp. 6 (2017)	15 Feb–1 Mar	14	R (1000) FR (1000) R:FR mix (1000) R:FR mix (2000) 1 h R (3000)* 1 h R-FR (3000)* 1 h R-FR-R (3000)* 1 min FR (3000)+ 1 min R-FR (3000)+ 1 min FR-R (3000)+ W (2800) D (0)	Asterix	9
Exp. 7 (2017)	30 Mar–20 Apr	21	UV-A 380 nm (1000) UV-A 400 nm (1000) B (1000) G (1000) R (1000) FR (1000) W (2800) D (0)	Asterix	9

*1 h R LED pulse every 3 h (followed by 10-min reversal periods of FR and R), 8 times per 24 h

+ 1 min R or FR pulses every 3 min (followed by 20-s reversals of FR or R), 50 times per 24 h

varied for different LED colours. Twelve tubers were measured per cultivar, light quality treatment and irradiance.

Sprout Growth Under a Broad Range of Wavelength Maxima

After finding that irradiances of around 1000 nmol m^{-2} s^{-1} were sufficient for inhibiting sprout growth in both the red and far-red light (exp. 2–3), we tested a slightly lower level 100 nmol m^{-2} s^{-1} in exp. 4 over a larger range of wavelengths including ultraviolet A (UV-A), blue, green, red and far-red in all four cultivars. Twelve tubers were measured per cultivar and light quality treatment. This setup was later repeated in exp. 7 in 2017 at higher irradiance (1000 nmol m^{-2} s^{-1}) in Asterix, in combination with an assay of the effects of different wavelength maxima on subsequent emergence and growth vigour in a pot experiment. Nine tubers were measured per light quality treatment in exp. 7.

Effects of Red and Far-Red Mixtures on Sprout Growth

Since wavelength maxima in both red and far-red were most effective inhibiting sprout growth, we set up an experiment using 1:1 mixture of continuous red and far-red light at very low fluence rates in exp. 5 in 2016. This was further tested at higher fluence rates in exp. 6 in 2017, with an addition of low, frequent 1 h pulses every third hour of red light, at equal molar quantities of light as in the continuous red light exposure. Subsequent 10-min durations of far-red and red light were also tested after the 1 h red pulse, for potential phytochrome-related reversals in responses. High, frequent pulses of 1 min far-red light every third minute were also tested, with 20 s reversals of red and far-red light. Due to a limited number of programmable events in the RX-30 units, it was only possible to have 50 min total of short pulses per day. Thus, the molar quantity of far-red light in the pulse treatments was reduced to only about 10% of that in the continuous light treatments. Twelve tubers were measured per cultivar and light quality treatment in exp. 5 and nine per treatment in exp. 6.

Growth Vigour Assay After LED Pre-treatments

Growth vigour of pre-sprouted tubers was tested 21 days after LED treatments in exp. 7 in 2017. Each of eight tubers per treatment with intact sprouts (except for the dark treatment) was planted at 5 cm depth in 2.0 L pots filled with a volume mixture of 75% fertilised peat soil and 25% perlite. Similarly, eight de-sprouted tubers from each treatment, and a sample of eight tubers directly from dark storage at 3.5 °C, were planted as references. However, all tubers from the dark treatment were de-sprouted due to very long and fragile sprout attachments.

The tubers were planted in pots on April 20 and grown in the greenhouse until June 12. The pre-treatment groups were randomly distributed in a greenhouse room with temperature set at a minimum of 15 °C. Pots were watered daily on demand. Date of emergence of sprouts was registered daily, height of the longest stem per pot was measured 22 days after planting (DAP) and plants were harvested 53 DAP. Stem numbers, stem dry matter, number of tubers (above 0.5 cm diameter) and tuber fresh matter were recorded at harvest.

Statistical Analyses

The statistical analyses were performed using Minitab® version 16.1.1 (Minitab Inc., State College, PA, USA). One-way ANOVA was used for analyses of effects of light quality treatments (including darkness and white fluorescent light controls) on sprout length in exp. 1, 6 and 7 for cv. Asterix. Experiments involving more than one cultivar (exp. 2–5) were analysed by GLM ANOVA, with cultivar (C) and light quality treatment (L) as fixed factors. Each cultivar was subsequently analysed separately, due to significant interaction ($P < 0.001$) between cultivar and light quality treatments. In addition, data (excluding darkness and white fluorescent controls) in exp. 2 and 3 were analysed with LED light quality (L) and irradiance rate (I) as fixed factors. The values for sprout length were transformed with the natural logarithm in cases of non-normal distribution for the experiments. In addition, pairwise comparisons were performed for all ANOVA analyses using Tukey's test with α set at 0.05.

Day of 50% emergence of sprouts (and the corresponding 95% fiducial interval) in the growth vigour assay (exp. 7) was estimated using the logistical probit regression (Minitab). This estimate was based on the dates with an accumulated number of pots with emerging sprouts, within each light quality treatment. The effects of light quality for the remaining growth vigour data were analysed by one-way ANOVA.

Results

Effects of Spectral Composition on Photomorphogenic Development

Exposure of pre-washed tubers of cv. Asterix to blue, red and far-red LEDs revealed a clear distinction in de-etiolation and development of green pigments in sprouts and tuber skin. Tuber sprouts exposed to far-red LED were still etiolated and the skin colour was still red after 23 days (Fig. 2a), being similar in colour to tubers in darkness (not shown). In contrast, tubers exposed to red (Fig. 2b) and blue LED (not shown) developed green sprouts and visibly darker skin. The intensity of green colour in sprouts and skin also increased with increasing irradiance of red light between 10 and 900 nmol m^{-2} s^{-1} (Online Resource 1), and was less intense in blue compared with red (not shown). A similar distinction between etiolated sprouts (and skin) in far-red light and de-etiolation/greening in the other tested LED wavelengths was observed in all subsequent experiments for all cultivars (not shown). The tested cultivars Folva, Mandel and Gullauge have yellow/pale skin colour, and thus had clearly visible greening in the skin when exposed to LED lights ranging from 380 to 660 nm, as opposed to darker skin in Asterix for the same wavelengths.

Fluence-dependent Suppression of Sprout Growth at Different Wavelengths

Exposure of pre-washed tubers of Asterix to blue, red and far-red LED light at 90 nmol m^{-2} s^{-1} (exp. 1) produced significantly shorter sprouts in far-red light than red light and about 2–3 times longer sprouts in blue light ($P < 0.001$). There was no significant difference in sprout lengths between tubers exposed to the red LED at 10, 30, 90 and 900 nmol m^{-2} s^{-1} in the same experiment. The subsequent experiment with

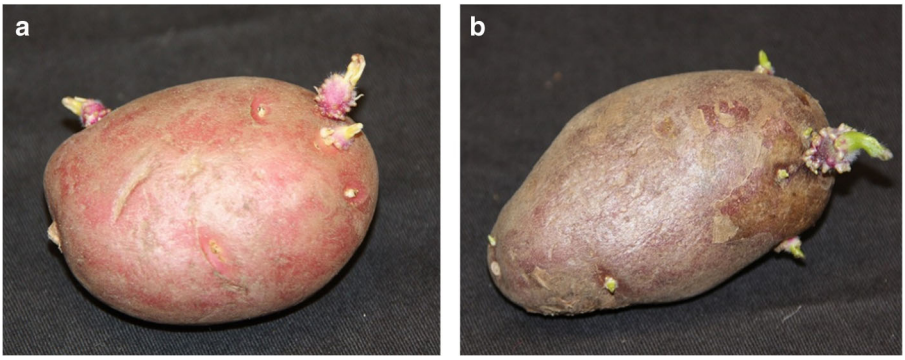

Fig. 2 Experiment 1 (2016). Distinct colour development in the skin and sprouts of pre-washed potatoes (cv. Asterix). **a** Remaining etiolated in far-red LED light (maxima 735 nm). **b** Greening in red LED light (maxima 660 nm)

cvs. Asterix, Folva, Mandel and Gullauge (exp. 2) revealed a fluence-dependent inhibition of sprout growth in blue, red and far-red light (Table 2). Far-red LED produced consistently shortest sprout length in all cultivars at the highest irradiance 1000 nmol m^{-2} s^{-1}, and at the lowest irradiance 10 nmol m^{-2} s^{-1}, red LED produced consistently shortest sprouts in all cultivars. Sprout length in white light in this experiment was also not significantly different from far-red at the highest irradiance for all cultivars, while dark control was not different from blue light at the lowest irradiance for three of the cultivars. This experiment was repeated once (exp. 3) with very similar results for all cultivars (data not shown).

Sprout Growth Under a Broad Range of Wavelength Maxima

Test-results using LED lights covering a broader range of maxima from 400 to 735 nm (exp. 4) also displayed the highest sprout length inhibition in red and far-red exposure (Table 3). Analysis of variance revealed a significant interaction between cultivar and LED colour ($P \leq 0.001$, 10 *df*, $n = 11–12$). The cultivars differed mainly in their relative response to red and far-red LEDs and differed less in the UV-A, blue and green part of the spectrum. The average sprout length was consistently shortest in far-red for all cultivars, yet it was only significantly shorter than in red light for Asterix.

The overall sensitivity to all the tested LED colours was quite high, with a minimum response of more than 50% inhibition of sprout elongation (relative to sprout growth in darkness) in all cultivars. A shorter duration of this experiment, with cv. Asterix at 380 to 735 nm and 120 nmol m^{-2} s^{-1} (exp. 7), also resulted in shortest sprout lengths in far-red followed by red wavelengths (Fig. 3). In addition, there was also a significant effect of UV-A LEDs at 380 nm and 400 nm, inhibiting sprout elongation more than in the blue region.

Effects of Combination of Red and Far-Red on Sprouting

In a test of the red and far-red LED at very low fluence (exp. 5), FR again was less effective than R at inhibiting sprout elongation in two of the cultivars (Table 4).

Table 2 Experiment 2 (2016). Average sprout length (mm) in potato cultivars at low and high irradiance rates of blue, red and far-red LED light. The standard error of mean is shown in brackets, and different lower-case letters within columns indicate significant difference by GLM ANOVA (Tukey 95%)

Irradiance/LED treatment	Asterix	Folva	Mandel	Gullauge
Control				
Darkness	120.0 (± 8.8)	110.7 (± 7.5)	30.0 (± 1.5)	21.2 (± 3.6)
White fluorescent+	14.9 (± 0.7)	11.8 (± 0.6)	7.4 (± 0.5)	8.4 (± 0.8)
n	11–12	11–12	11–12	10–12
10 nmol m^{-2} s^{-1}				
Blue 450 nm	110.1 (± 4.2) a	71.8 (± 4.8) a	25.8 (± 1.7) a	23.1 (± 3.1) a
Red 660 nm	30.3 (± 3.6) c	13.8 (± 0.7) bc	9.2 (± 0.2) c	16.5 (± 1.7) ab
Far-red 735 nm	54.7 (± 4.2) b	18.4 (± 3.2) b	11.7 (± 0.5) b	23.1 (± 3.3) a
1000 nmol m^{-2} s^{-1}				
Blue 450 nm	19.6 (± 0.8) d	14.4 (± 1.0) bc	8.6 (± 0.4) c	12.8 (± 0.6) bc
Red 660 nm	19.6 (± 1.9) d	14.8 (± 0.6) bc	8.2 (± 0.3) c	12.1 (± 1.1) bc
Far-red 735 nm	12.1 (± 0.5) e	11.7 (± 0.6) c	6.5 (± 0.3) d	9.3 (± 0.5) c
n	10–12	10–12	12	9–12
P value				
Light quality (L)	< 0.001	< 0.001	< 0.001	0.084
Irradiance (I)	< 0.001	< 0.001	< 0.001	< 0.001
(L × I)	< 0.001	< 0.001	< 0.001	0.032

+ Irradiance rate at 2.8 μmol m^{-2} s^{-1}

Table 3 Experiment 4 (2016). Average sprout length (mm) of potato cultivars exposed to different wavelength maxima of LED light at 100 nmol m^{-2} s^{-1} for 21 days at 15 °C. Standard error of mean is shown in brackets, and different lower-case letters within columns indicate significant difference by one-way ANOVA (Tukey 95%)

Treatments	Asterix	Folva	Mandel	Gullauge
LED				
UV-A 400 nm	50.4 (± 4.3) b	25.9 (± 2.9) bc	14.9 (± 0.6) b	24.6 (± 4.3) a
Blue 450 nm	67.6 (± 4.9) b	29.0 (± 3.3) b	15.2 (± 1.2) b	19.2 (± 2.5) ab
Green 520 nm	64.0 (± 5.6) b	23.3 (± 2.6) bc	14.3 (± 0.7) b	24.1 (± 3.5) a
Red 660 nm	28.5 (± 3.0) c	19.4 (± 2.1) cd	9.7 (± 0.5) c	13.5 (± 0.8) bc
Far-red 735 nm	13.6 (± 0.8) d	13.1 (± 0.6) de	8.5 (± 0.4) c	10.0 (± 1.0) c
n	11–12	12	12	9–11
Control				
Darkness	131.0 (± 10.7) a	125.8 (± 10.3) a	46.8 (± 10.6) a	56.0*
White fluorescent+	14.1 (± 0.5) d	12.2 (± 0.4) e	8.9 (± 0.5) c	8.6 (± 0.4) c
n	9–12	12	5–12	1–10
P value	< 0.001	< 0.001	< 0.001	< 0.001

+ Irradiance rate at 2.8 μmol m^{-2} s^{-1}

*Gullauge: $n = 1$ (due to apical necrosis)

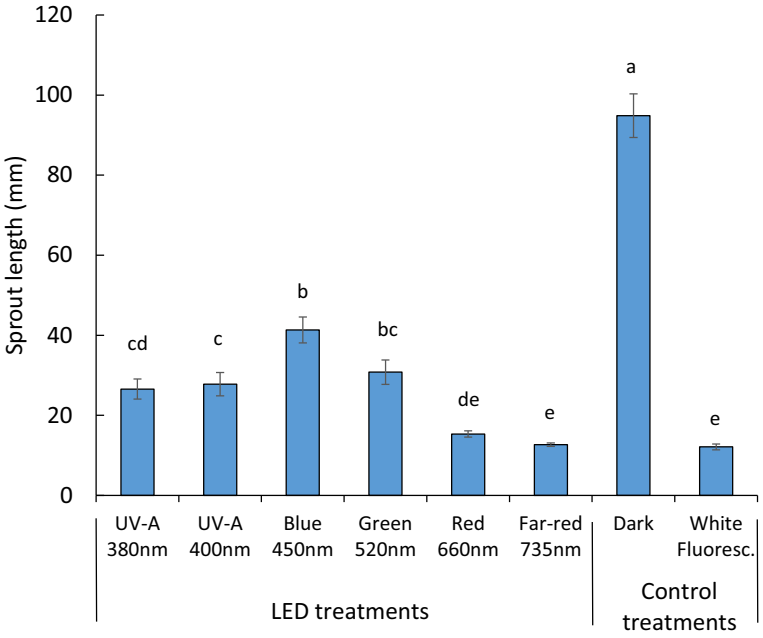

Fig. 3 Experiment 7 (2017). Average sprout length (± SEM) of potatoes (cv. Asterix) exposed to different wavelength maxima of LED light at 120 nmol m^{-2} s^{-1} for 21 days at 15 °C. White fluorescent light control at 2.8 μmol m^{-2} s^{-1}. A significant difference between LED treatments (Tukey 95%) is indicated by lower-case letters. Sample size ($n = 9$) for all treatments, except for darkness control treatment ($n = 7$)

Combining FR and R in a 1:1 mixture did not significantly add to the inhibition seen for R light alone (Table 4). This was true for all four tested cultivars, in spite of an increase in total irradiance from 10 to 20 nmol m^{-2} s^{-1}. At higher irradiance for cv. Asterix (exp. 6), combinations of R:FR again did not produce significant differences in sprout length compared with either single R or FR exposure (Fig. 4). This was regardless of whether total irradiance was kept constant at 1000 nmol m^{-2} s^{-1} or doubled to 2000 nmol m^{-2} s^{-1}. Still, when comparing continuous FR exposure versus continuous R only, there were slightly shorter sprouts in FR light ($P = 0.039$, $n = 18$). All mixtures containing red light induced visible greening of sprouts (data not shown).

Pulsed sequences of R and FR every third hour, designed to induce photo-reversible phytochrome B types, did have an influence on sprout length in Asterix (Fig. 4). Inclusion of 10 min FR pulses directly after 1 h R pulses did not reduce lengths compared with 1 h R pulses only. However, a further insertion of another 10 min of R directly after the FR, significantly shortened the average sprout length by 3.8 mm. On the other hand, shorter 60 s pulse treatments designed to induce light-labile phytochrome A type had little effect on sprout length (Fig. 4). LED treatments with high, frequent 60 s FR pulses every third minute followed by 20 s R pulses did not reduce the sprout length significantly compared with 60 s FR only. In addition, there was also no observable reversal in colour development in any of the LED pulse experiments (not shown). All pulse treatments with red LED developed green colour in sprouts, and all treatments with subsequent pulsed reversals ending with FR were still green and not etiolated.

Table 4 Experiment 5 (2016). Average sprout length (mm) in potato exposed to very low fluence LED red (R), far-red (FR) or a (1:1) mixture of these, $n = 10–12$ (except for dark control treatments which were $n = 6–7$ and none for Gullauge). The standard error of mean is shown in brackets, and different lower-case letters within columns indicate significant difference by one-way ANOVA (Tukey 95%)

Treatments	Asterix	Folva	Mandel	Gullauge
LED				
Red 660 nm	16.4 (± 1.6) c	14.3 (± 1.4) bc	8.0 (± 0.6) bc	12.1 (± 0.8) b
Far-red 735 nm	25.0 (± 3.0) b	16.8 (± 1.0) b	10.8 (± 1.3) b	18.8 (± 1.7) a
Red:far-red (1:1)	11.8 (± 0.7) cd	11.8 (± 0.3) cd	8.3 (± 0.6) bc	11.2 (± 1.1) b
n	11–12	12	12	10–12
Control				
Darkness	75.8 (± 8.9) a	51.0 (± 7.3) a	22.1 (± 2.4) a	–
White fluorescent[+]	10.2 (± 0.6) d	10.5 (± 0.3) d	6.2 (± 0.4) c	7.3 (± 0.4) c
n	6–12	6–12	7–12	0–10
P value	< 0.001	< 0.001	< 0.001	< 0.001

[+] Irradiance rate at 2.8 μmol m^{-2} s^{-1}

Growth Vigour Assay After Exposure to a Broad Range of LED Maxima

There were no significant differences in plant emergence when pre-treated with any of the LEDs between 380 and 735 nm, after planting tubers with intact sprouts (Fig. 5).

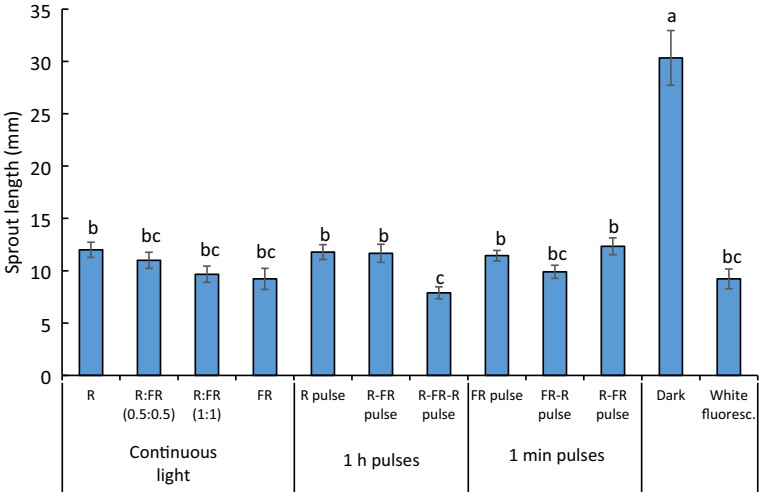

Fig. 4 Experiment 6 (2017). Average sprout length of potato (cv. Asterix) at continuous or pulsed exposure of red (R) and far-red (FR) LED. Continuous treatments were either single R or FR at 1.0 μmol m^{-2} s^{-1}, or R:FR mixtures at 1.0 and 2.0 μmol m^{-2} s^{-1}. Pulse treatments at 3.0 μmol m^{-2} s^{-1} were either long (1 h every 3 h, 8 times per day) or short (1 min every 3 min, 50 times per day). Long pulses were 1 h R, 1 h R followed by a 10 min FR reversal, or 1 h R followed by 10 min FR and 10 min R-reversal. Short pulses were 1 min FR, 1 min FR followed by a 20 s R-reversal, or 1 min R followed by a 20 s FR reversal. White fluorescent light at 2.8 μmol m^{-2} s^{-1} and darkness as control reference. Error bars indicate ± standard error mean, and significant difference in one-way ANOVA (Tukey 95%) is indicated by lower-case letters. Sample size ($n = 9$) for all treatments

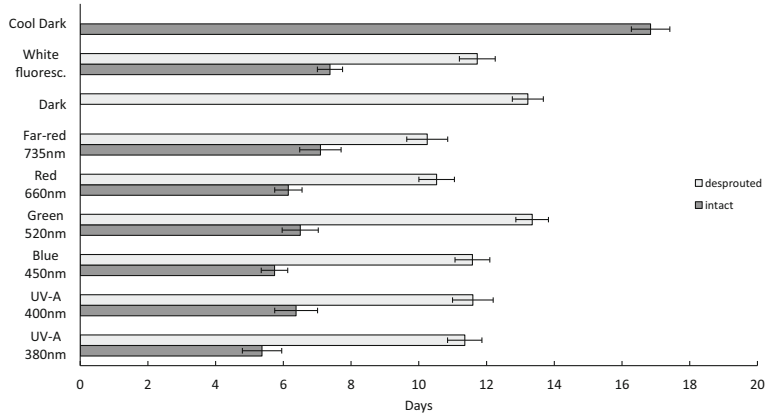

Fig. 5 Experiment 7 (2017). Days to 50% emergence (probit) from the soil after planting of seed potatoes (from the same treatments as in Fig. 3) in a greenhouse pot experiment. Seed tubers were planted with either intact sprouts or de-sprouted. Seed tubers directly from cold storage (cool dark) as reference. Sample size within each group was $n = 8$, and 95% fiducial intervals are indicated with bars

Also, at harvest, 53 DAP, there was no difference in plant height, number of stems, shoot dry matter content, number of daughter tubers (< 3-mm diameter) and tuber fresh mass (Online Resource 2). For de-sprouted tubers, however, plant emergence was significantly earlier after red and far-red exposure, compared with other LEDs. Tubers exposed to green LED and darkness emerged later from the soil compared with all other treatments. These differences were still not large enough to produce differences at harvest in plant height, number of stems, shoot dry matter content, tuber numbers and tuber FM, except for green LED which produced lower tuber FM (Online Resource 3).

Discussion

The results clearly demonstrate a potential for using LED light systems to inhibit sprout growth in green-sprouting of potato seed tubers. LEDs in the red and far-red part of the spectrum produced short sprouts in all cultivars, comparable in length with those of fluorescent light control treatments at 3–5 times higher total irradiance. This irradiance difference may, over a normal green-sprouting period of 6–8 weeks, further reduce power consumption and energy costs for illumination. This is in addition to the benefit of two times higher quantum efficiency of LEDs, compared with fluorescent or incandescent light sources (Schubert and Kim 2005). The similar response to sprout growth inhibition under red and far-red light, and a lack of greening in far-red light, suggests a common underlying photomorphogenic mechanism in potato tubers at these wavelengths. The relative differences in sprout lengths between cultivars for some LED colours may reflect cultivar differences in sensitivity to light or be due to differences in their growth potential (McGee et al. 1988a). Nevertheless, LEDs enriched in the upper part of the visible spectrum and far-red could be useful universally among cultivars for green-sprouting.

The observed wavelength dependence for inhibition of sprout elongation in the LED treatments agrees largely with sensitivity reported by McGee et al. (1987b). Both

studies indicate different sensitivity ranges for red and far-red light, with highest sensitivity to far-red light (down to low irradiances of 100 nmol/m^2/s) and highest sensitivity to red LED light at very low irradiances (10 nmol/m^2/s). McGee et al. (1987b) identified maximum inhibition around 707 nm in the far-red region, which is lower than our LED in far-red at 735 nm. Thus, it is possible that LEDs with lower wavelength maximum in the far-red region may be even more effective. Highest photon effectiveness has also been shown at 712 nm, for phytochrome/cryptochrome-associated flower induction in *Fragraria chiloensis* (Yanagi et al. 2016). In contrast to McGee et al. (1987b), we observed low sensitivity to blue LED at 450 nm. This may be due to cultivar differences, as the response to either blue or green LED varied in being least effective among our tested cultivars. There were also some indications that UV-A may inhibit sprout growth more than blue/green in our experiments. More energetic UV-C (at 254 nm) in short durations has been shown to inhibit sprout growth in potato (Cools et al. 2014). However, this may have limited practical relevance for green-sprouting potato seed tubers, as UV LEDs have much lower quantum efficiency than LEDs in the visual part of the spectrum (Cooke 2010). Furthermore, LED light in far-red was more efficient than UV-A at irradiances as low 100 nmol m^{-2} s^{-1} in inhibiting sprout growth. Until further studies have been done on different cultivars' sensitivity over full 6–8-weeks green-sprouting period, we recommend continuous irradiances of specific red/far-red LED of at least 1 μmol m^{-2} s^{-1} during pre-sprouting.

The observed lack of greening under far-red light is interesting from a plant development perspective, as seedlings of other species usually respond to very low fluences of far-red light by de-etiolation (Takano et al. 2005). This suggests that photomorphogenesis and de-etiolation in the vegetatively propagating potato tubers may be different from in seedlings. McGee et al. (1987a) also reported a lack of green colour in cv. Maris Piper under far-red light. However, in another study, Desiree developed green colour in emerging sprouts from soil under far-red light (Heyer et al. 1995). This allows for a possibility of a conditional de-etiolation response in tubers, depending on whether sprouts are drawing nutrients from the soil or are relying purely on the reserves in the tuber organ. In the latter study of cv. Desiree, induced greening was positively influenced by phytochrome A levels (Heyer et al. 1995). Our observation of increasing green colour strength in sprouts and potato skin upon increasing irradiance, and lack of red to far-red reversibility is indeed in agreement with a saturated high irradiance response of phytochrome type A function in seed tuber sprouts.

The inhibition of tuber sprout growth across all the tested LED maxima falls within documented absorption and action spectra of phytochromes (Butler et al. 1964; Seyfried and Schäfer 1985). Furthermore, the observed different sensitivity ranges to red and far-red light and different de-etiolation response between these wavelengths indicate an involvement of two (or more) phytochrome types in seed tuber sprouts. Sensitivity at lower irradiance of red light fits with described very low fluence responses of phytochrome A and sensitivity at higher irradiance of far-red light agree with low fluence responses of phytochrome B (Shinomura et al. 1996; Takano et al. 2005; Xie et al. 2007). The potato genome contains five different phytochrome genes (A, B1, B2, C and E) (The Potato Genome Sequencing Consortium et al. 2011), and so far, only effects of phyA have been investigated in potato sprouts reducing sprout elongation in far-red light (Heyer et al. 1995). The observed lack of any additional

inhibitory effect of mixing red and far-red light in continuous exposures or pulses at equivalent light quantity supports the notion of a saturation/HIR mediated by phytochrome (in potato sprouts). For inhibition of sprout elongation during green-sprouting, this means that given a sufficient quantity of light for maximum inhibition, the duration of daily light exposure is not important. This is supported by previous studies of broad-spectrum fluorescent light at photoperiods down to 1 h and 8 h (McGee et al. 1987a; Johansen and Mølmann 2017).

The earlier emergence from the soil of de-sprouted seed tubers, pre-treated with red and far-red compared with the other LEDs, may suggest a wavelength-specific influence on tubers during pre-sprouting. However, this difference was only 2–3 days ahead of the darkness control and not sufficient to affect subsequent growth and tuberisation 53 DAP. Furthermore, in the unsprouted tubers, the LEDs producing the longest sprouts also emerged earliest from the soil. Sprout length can thus have a greater effect on stem biomass and earlier yield than different LED colour exposures. This, of course, will be limited by the ease of detachment in long sprouts during planting. Light has also been shown not to affect dormancy release in potato (McGee et al. 1987a), and in a similar comparison of de-sprouting from light versus darkness, there were also no significant effects on the emergence and later yield in-field performance of different cultivars (McGee et al. 1988b). It may seem that the choice of light colour during pre-sprouting phase does not have an influence on subsequent growth and yield, although this also needs to be tested for LEDs in field trials. A lack of influence of LED colour on subsequent growth and yield is in agreement with temperature as the main influence on physiological ageing in seed tubers (Blauer et al. 2013).

In conclusion, our results demonstrate the potential for utilising LEDs of specific red and far-red light during green-sprouting for maximum inhibition of sprout growth. Inhibition of sprout elongation and greening of sprouts display a dose-dependent or saturation response with increasing light flux, with no additive effects of mixing red and far-red light. Based on the results, we recommend continuous irradiances of specific red/far-red LEDs at a minimum 1.0 μmol m^{-2} s^{-1}, or alternatively, equal dosage per day may be applied for shorter daily durations. The underlying mechanism for these responses involves at least two photo-receptor systems, possibly involving different phytochrome types or photo-isomers.

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