

MINI REVIEW

Influence of Arctic light conditions on crop production and quality

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Funding information

Grofondet, Grant/Award Number: 190028; NordForsk, Grant/Award Number: 84597; Norges Forskningsråd, Grant/Award Number: 296397

Edited by V. Hurry

Abstract

The natural light conditions above the Arctic Circle are unique in terms of annual variation creating special growth conditions for crop production. These include low solar elevations, very long daily photosynthetic light periods, midnight sun/absence of dark nights, and altered spectral distribution depending on solar elevation. All these factors are known to affect the growth and the metabolism of plants, although their influence on northern crop plants has not yet been reviewed. The ongoing global warming is especially affecting the temperature × light interactions in the Arctic, and understanding the impact on crop production and plant metabolism will be important for an Arctic contribution to global food production. Arctic light conditions have a strong influence on the timing of plant development, which together with temperature limits the number of cultivars suitable for Arctic agriculture. This review compiles information from the reports about the effects of light conditions at high latitudes on growth, biomass production, flowering and quality of the crop plants and discusses the gained knowledge and the key gaps to be addressed.

1 | INTRODUCTION

Solar radiation above the Arctic Circle ($66^{\circ}33'48''$ N) in summer includes a midnight sun period of 24-h photoperiod and very long daily photosynthetic light periods, as well as some characteristic diurnal spectral distributions depending on solar elevation. Most of the land mass above the Arctic Circle is presently locked in permafrost, except for northern Norway, Sweden, Finland, and parts of north-western Russia (Obu et al., 2019, Figure 1). In this area, the heat energy of the Norwegian Ocean Current enables crop production at

up to $70\text{--}71^{\circ}\text{N}$, at higher latitudes than elsewhere on the planet. The unique light conditions at these latitudes together with relatively low growth temperature can influence growth, development, and quality. Under the predicted global warming these light conditions also have a potential for increased production. This region shares similar climatic temperature-zone as in Sub-Arctic latitudes of Iceland, Greenland, Canada, United States, and Russia. These sub-Arctic areas contain many of the features of light conditions found above the Arctic Circle, with a gradual decrease in similarity with decreasing latitude below it. To avoid possible confusion with the Arctic climate definition, this

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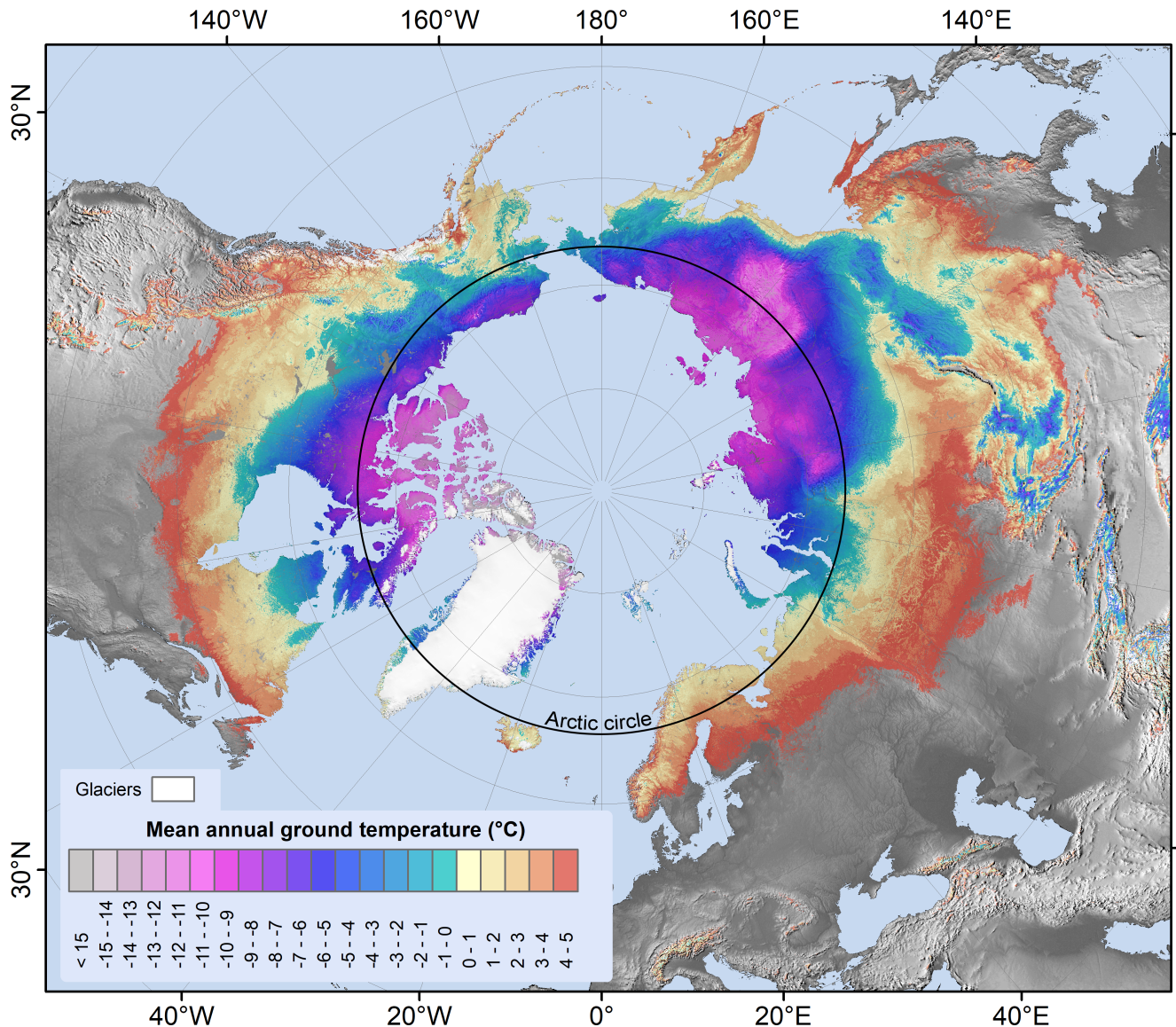


FIGURE 1 Map of permafrost extent and ground temperature, 2000–2016 in Arctic and sub-Arctic regions (adapted with permission from Obu et al., 2019, Alfred Wegener Institute, Helmholtz Centre for Polar and Marine Research, Bremerhaven, PANGAEA, <https://doi.org/10.1594/PANGAEA.888600>)

review will only refer to Arctic and Sub-Arctic light conditions as defined by the Arctic Circle.

The short frost-free summers at high latitudes permit production of mainly low-temperature-adapted crops like potato, vegetables, berries, and fodder. Because of global warming, Arctic areas are likely to have increasing importance for global food production, as new species and cultivars with higher temperature optimums and higher yield may be grown due to warmer and extended growing season with earlier crop establishment in the spring. Local projections for Northern Norway indicate that the growing season will extend by 1–4 weeks in 2021–2050 compared to the reference period 1961–1990 (Uleberg et al., 2014). The largest increase is predicted for inland and in the northernmost regions, under most extreme scenarios with up to 2 months longer growing season in Northern Norway (Hanssen-Bauer

et al., 2015). However, at higher latitudes, this increase will mostly extend the spring season due to the rapid shortening in day length in autumn. It is difficult to predict land use changes due to altered northern climatic zone limits. Still, larger areas will be available in the Arctic with a climate suitable for plant production in the future. Hanssen-Bauer et al. (2015) estimated that the increase in area with growing season more than 180 days has been from 37,000 (1971–2000) to 45,000 km² (1985–2014) in Norway. Furthermore, depending on the temperature increase, release of also sub-Arctic areas from permafrost may open up new areas for agriculture in the northern hemisphere, in northern Canada/United States, and Russia. Knowledge about adaptations and challenges due to light conditions will therefore be necessary to meet future changes. This review aims to discuss the special light conditions at high latitudes, their reported effects on crop

production and quality, and key gaps to be addressed for future development of agriculture at high latitudes.

1.1 | Arctic solar environment

Globally the declination angle of the Sun's path across the sky changes in the course of the orbital year between $+23.45^\circ$ and -23.45° , due to Earth's tilted rotational axis in relation to its orbital plane. In the northern hemisphere, this translates to increasing photoperiods and daily solar elevations (relative to the horizon) from winter solstice (December 21–22) to summer solstice (June 20–21), and conversely, decreasing photoperiods and solar elevations from summer to winter solstice (Figure 2). At Arctic latitudes, there is in addition an increasing dampening (with latitude) in the diurnal amplitudes between solar elevations at solar noon and at solar midnight.

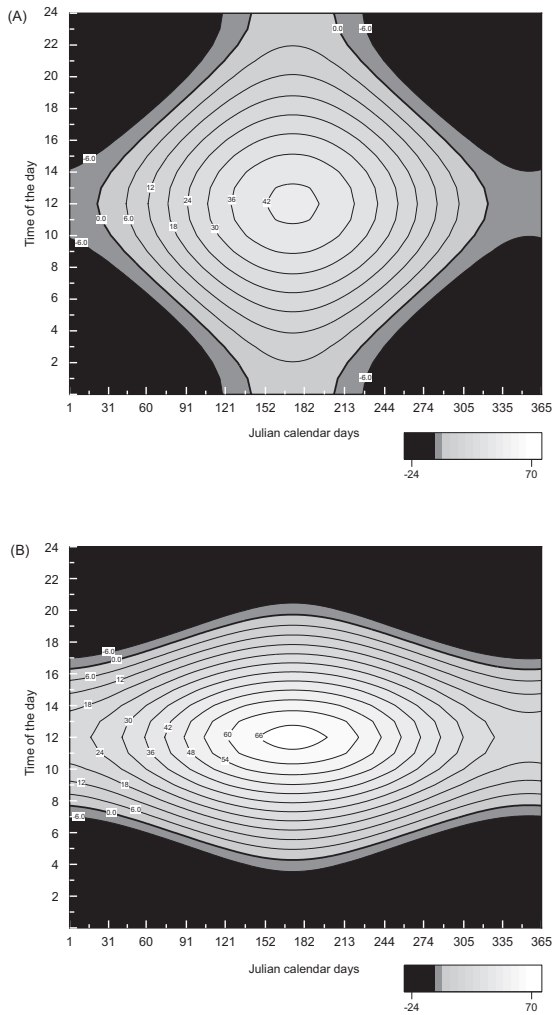


FIGURE 2 Diurnal variation in solar elevation angle throughout the year (A) above the Arctic circle at 70°N and (B) at 45°N . Julian calendar day plotted as x-axis against time of the day in y-axis with degrees of elevation angles indicated in white boxes. The elevation angles between 0° and -6° indicate civil twilight and transitions for every 6th degree are indicated by numbered contour lines

Locations above the Arctic Circle are therefore subject to a midnight sun period in summer where the Sun does not set below the horizon, and a polar night period in winter where it does not rise. These periods increase in duration with increasing Arctic latitude.

The solar radiation is attenuated more through the atmosphere at high latitudes compared to lower latitudes, due to the lower solar elevation angles and thus longer path length through the atmospheric column. Atmospheric constituents reduce radiation by absorption (from aerosols and ozone), Rayleigh scattering (by oxygen and nitrogen molecules), and Mie scattering (reflection from cloud tops) (Gates, 1980). Both absorption and Rayleigh scattering are wavelength specific. The angle of incidence/path length therefore also strongly influences the spectral quality of the light for different solar elevations, in addition to reductions in direct radiation (Figure 3). For low solar angles, this means that ozone selectively filters out more UV radiation than at higher solar angles. There is also more effective scattering of blue light versus red light in the atmosphere at low angles, since the resonant frequencies of oxygen and nitrogen molecules are highest in the UV-blue part of the spectrum.

Light conditions in summer at Arctic and sub-Arctic latitudes, which may influence plant development, include: (1) low solar maximum elevations, (2) absence of darkness at night, (3) very long daily photosynthetic light periods, and (4) diurnal spectral distributions in UV, blue, red, and far-red light. For low maximum solar elevations at high latitudes, this means that the same unit of surface area generally receives lower insolation (irradiance \times time) than at lower latitudes. Consequently, temperatures are lower and the growth season shorter at high latitudes, with average temperatures as low as $10\text{--}12^\circ\text{C}$ in June–August (Hårdh et al., 1977). The absence of darkness at night at high latitudes is likely to affect development and biochemistry

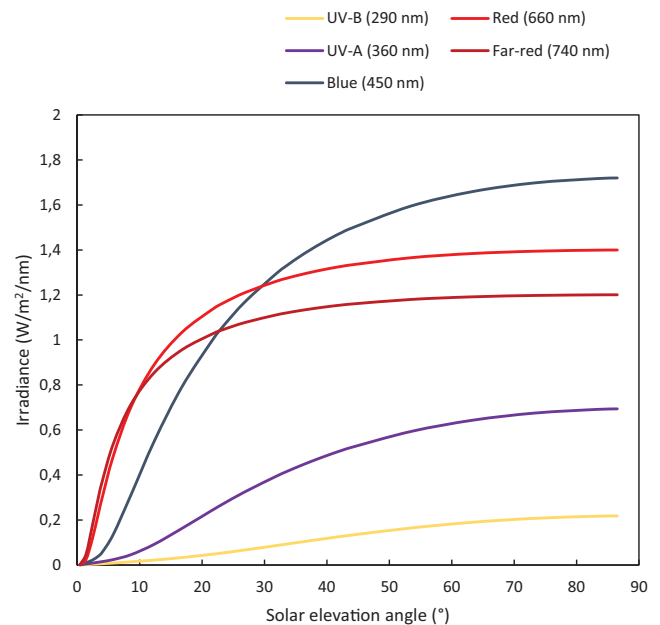


FIGURE 3 Irradiance (SPCTRAL2[Bir86]) at different solar elevations relative to the horizon for UV-A, UV-B, blue, red, and far-red light at 290, 360, 450, 660, and 740 nm, respectively

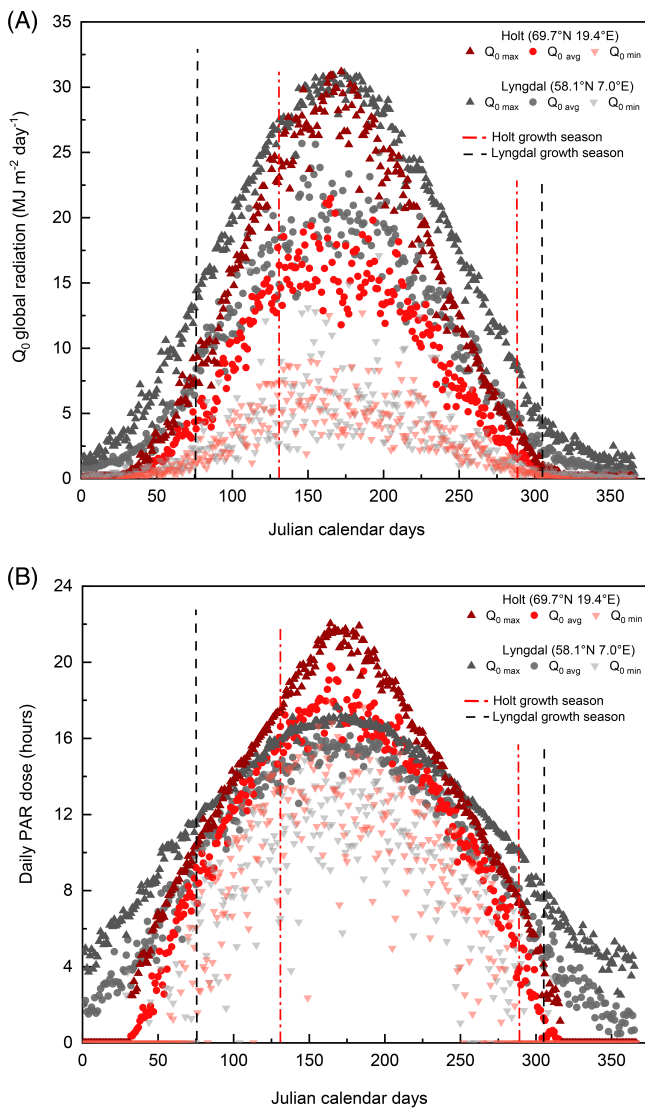


FIGURE 4 The daily averages, maximums, and minimums (2011–2020) of global solar radiation (A) and estimated daily period of photosynthetically active radiation (PAR) (B), from two sites in Norway at Holt (69.7°N) and at Lyngdal (58.1°N). The radiation data were obtained from agricultural meteorological stations of the Norwegian Institute of Bioeconomy research (NIBIO) (<https://lmt.nibio.no/>), and PAR periods were based on daily durations of global radiation above 50 W m^{-2} . The average start of the growth season is indicated in dotted dashed lines to the right and the first incidence of Autumn frost to the left

dependent on diurnal light/dark cycles, as indicated in studies of in natural populations of high latitude origin (Junttila, 1980). Even though the total radiation may be similar across latitudes mid-summer, the photosynthetic light period is longer at high latitudes (Figure 4). During the midnight sun period, this can result in up to 25–26% photosynthetic accumulation at night in Arctic species (Semikhatova et al., 1992). However, the challenge for crop production in the Arctic is to develop mature harvest, before the more rapid drop in solar elevation and temperatures in autumn, compared to longer and warmed autumn periods at southern latitudes. Finally, the diurnal light

spectrum at high latitudes with lower solar elevation angles varies differently in relative contents of UV, blue, and red/far-red, compared to lower latitudes with higher elevation angles (Figure 3). The level of direct UV-radiation reaching the ground is lower during the day in the north (Zoratti et al., 2014). At night, above the Arctic Circle, there are also prolonged periods when the Sun is between 0 and 5° , and the radiation is refracted and scattered through a longer atmospheric path, lowering the energy distribution toward long wavelength far-red light (Nilsen, 1985).

1.2 | Plant perception of Arctic light conditions

Plants detect changes in the light environment, including irradiance, light quality, and photoperiod, either directly through changes in the redox-status of the photosynthesis apparatus and metabolism, or through specialized light receptors with high sensitivity in distinct regions of the light spectrum. The reaction centers of the photosystems within the chloroplast membrane receive energy in form of photons, feeding the process of photosynthesis in CO_2 assimilation and producing energy. The energy expressed as excitation pressure within the photosystem also has an important role in signal transduction for gene expression (Hüner et al., 2014). High excitation pressure in PSII is involved in signaling start of growth cessation when temperature drops during late summer, and in initiation of photoacclimation for protection against photoinhibition (Hüner et al., 2012). Photosynthesis can also affect photoperiodism by altering the circadian rhythms of internal clock factors (Haydon et al., 2013). It has not yet been studied in detail how the very long daily photosynthetic light periods or redox signaling in the Arctic may affect circadian rhythms in plants.

For plants, light is not only the source of energy for photosynthesis but also a signal for growth and development including photoperiodic control of leaf/flower orientation, flowering, dormancy, and germination. Specific photoreceptors sense changes in light conditions and their output are often integrated with other signaling pathways and/or endogenous rhythms, by gene transcription and protein modification. There are currently five main classes of photoreceptors described in plants: phytochromes, cryptochromes, phototropins, the ZLP/FKF/LKP/ADO family, and a UV-B receptor (Björn, 2015). Red and far-red light are primarily detected by the phytochrome system in the plants, with activity determined by photo-isomeric conversion(s) between red light absorbing (Pr) form and far-red absorbing (Pfr) form, in addition to protein-modification and selective degradation of phytochrome proteins (Smith, 2000). Phytochromes together with blue-light detecting cryptochromes are the main photoreceptors involved in photoperiodic responses. In temperate and boreal zones, termination of growth and bud-set in trees is induced by increasing night lengths (Olsen et al., 1997). However, different mechanism may control growth cessation in trees adapted to continuous light conditions at high latitudes. It has been suggested that the change in light quality expressed as R:FR ratio may be of similar significance for growth cessation in the Arctic (Nilsen, 1985), as observed for sensitivity of flowering in cocklebur across the narrow R:FR range of 1.10–1.03

(Salisbury, 1981). A low R:FR ratio as part of 24-h photoperiod is necessary to maintain growth and prevent terminal bud set of *Picea abies* provenances from high latitudes (Clapham et al., 1998; Mølmann et al., 2006) and initiation of subsequent cold acclimation in dogwood (*Cornus stolonifera*) (McKenzie et al., 1974). However, the precise influence and interplay of UV, blue, and red/far-red light and critical thresholds for day- or night-timekeeping remains to be identified under natural Arctic light conditions.

Several light-responsive transcription factors in plants have been identified (Jiao et al., 2007) and some are responding to one type of light while others can respond to a wide spectrum of light. Downstream of photoreceptors, the E3 ubiquitin ligase COP1/SPA (CONSTITUTIVE PHOTOMORPHOGENIC 1/SUPPRESSOR OF PHYTOCHROME A-105), is a key repressor of photomorphogenesis targeting many positive regulators of light signaling, mainly transcription factors, for degradation in darkness (Hoecker, 2017). It will be interesting in future studies of both cultivated and wild plants to determine the relative importance in Arctic light conditions of photosynthetic light period, photoperiodic, and/or light quality detection coupled to endogenous diurnal rhythms and thresholds for plant development.

1.3 | Arctic growth conditions and biomass production

Cold-adapted grassland perennials used for milk and meat production dominate biomass production in Arctic agriculture. Despite the short and cold growing season, cultivation of potatoes and vegetables like carrots and Brassica species is of economic importance but covers only 1–2% of cultivated land area. Production of cereals has a long history in the north, but it is now quite limited in the Arctic and sub-Arctic area. However, due to warmer and longer growing seasons in recent years, there are efforts for re-introduction of cereal production. The optimum growth temperature for timothy and other most commonly grown forage grasses in northern areas is 18–22°C (Baker & Jung, 1968). However, temperature requirement for plant development generally decreases with increasing day length, so less accumulated growing degree days are needed to reach a given biomass at higher than at lower latitudes (Bootsma, 1984). So, despite of the low temperature, the rate of biomass production is often higher at high latitudes compared to lower latitudes, and grasses can reach up to 25 g m⁻² day⁻¹ around 70°N under favorable conditions in mid-summer (Simonsen, 1985). However, controlled studies have mostly focused on how long photoperiod may contribute per se to biomass, keeping the photosynthetic light period constant across experimental treatment groups. The stimulation of biomass production by day length extension is greatest in high-latitude grasses at low to moderate temperatures ($\leq 15^{\circ}\text{C}$), which are below the optimum growth temperatures of temperate grasses (Heide et al., 1985). Heide (1982), for example, demonstrated that during 5-week growth period at average temperatures (12–21°C), 24-h photoperiod compensated for more than 3°C in dry weight accumulation of timothy cultivars compared to 10-h photoperiod treatment. Growth stimulation by day length extension is not only confined to forage crop varieties adapted to high

latitude but is also true for a wide range of Northern European grasses. Similar effects have also been observed for several timothy, *Poa alpina* and white clover varieties of broad latitude origins (52–69°N) (Bertrand et al., 2008; Hay & Pedersen, 1986; Junttila et al., 2006; Solhaug, 1991). The basis for the photoperiodic stimulation in grasses of growth is a greater leaf area in long days (LDs) compared to short days (Heide et al., 1985; Wu et al., 2004). Hay and Pedersen (1986), Solhaug (1991), and Wu et al. (2004) demonstrated a greater increase in biomass production in northern-adapted cultivars compared to cultivars from lower latitudes as a response to day length extension. Heading of grasses at low temperature conditions at high latitudes can be substantially delayed (Heide et al., 1985), which can increase the biomass production because of a prolonged vegetative phase.

Few studies have focused on investigating the effect of Arctic light conditions on biomass production in annual crops such as vegetables. Some studies show no significant effect of photoperiod by itself on biomass production in broccoli (Steindal et al., 2013) and kale (Steindal, Rødven, et al., 2015). On the other hand, leaf length, leaf areas, and fresh and dry weight of radish and lettuce plants generally increased with increasing day length/irradiance, up to 20 h (Inada & Yabumoto, 1989). Furthermore, sugar beet also responded to both photoperiod and increased daily photosynthetic period, with increased leaf area and plant biomass (Milford & Lenton, 1976). In addition, nursery production of plant materials under Northern growth conditions has demonstrated higher growth performance related to photoperiod \times temperature as seen for strawberry crowns (Tanino et al., 2006). Most annual crops grown at high latitudes are imported from more southern regions and/or are day-neutral, and therefore may not respond directly to long photoperiods in the Arctic. Still, when the cultivar is adapted to the low growth temperatures, they can develop yields more rapidly under the very long photosynthetic light periods at high versus low latitude light conditions, as exemplified by broccoli and rutabaga (Johansen et al., 2017; Mølmann et al., 2018). The rise in temperature at higher latitudes will imply lengthening of the growing season especially in the spring, i.e. in late May and early June at Arctic region. At the time when solar elevation is close to the highest yearly values (Figure 2) and longest photosynthetic light periods (Figure 4), predicted higher temperatures can increase the biomass production in Arctic areas, as well as including species and cultivars with higher temperature optimums for growth (Uleberg et al., 2014). Low-temperature-tolerant plants also possess some plasticity in ability to acclimate the photosynthesis apparatus to warmer growth temperature (Mawson et al., 1986). Today, there is less plant pests at the high latitudes, but rising temperatures will likely bring novel plant pests to the Arctic region causing new challenges for crop production.

1.4 | Regulation of growth cycle in Arctic agriculture

Arctic climate with a short growing season and long days (LDs) sets special requirements for plants to control their yearly growth cycle.

Since accurate developmental timing of yearly growth cycle is important for survival and successful reproduction, plants have evolved sophisticated molecular mechanisms to monitor and respond to seasonal cues including changes in light and temperature. The best-known example is photoperiodic flowering that involves sensing of light using various photoreceptors, accurate diurnal regulation of *CONSTANS* (*CO*) mRNA and protein levels in leaves, *CO*-dependent activation of *FLOWERING LOCUS T* (*FT*) under inductive conditions, and the transport of *FT* protein through phloem to the shoot apical meristem to induce flowering (reviewed by Andres & Coupland, 2012). Similar mechanisms also control other photoperiodic responses including, for example, growth cessation and bud set in trees (Böhlenius et al., 2006) and tuberization in potatoes (Navarro et al., 2011). For plants, day length is the most reliable indicator of the season, and strong latitudinal clines in the photoperiodic responses of many species are found (Heide, 1985).

In the arctic, perennials that are able to form flower buds in autumn and to flower rapidly after snow-melt in the spring predominate. For example, 92% out of 169 flowering plants growing in northeast Greenland produce overwintering flower primordia (Sørensen, 1941). Typically, decreasing photoperiod and/or cool temperature (vernalization) trigger flower induction in autumn, but many temperate perennial grasses also require LD in the spring for inflorescence growth (Heide, 1985, 1994). In northern grass accessions, flower induction can take place in longer photoperiods than in southern accessions (Heide, 1994). Molecular mechanism of this LD adaptation is not known in arctic grasses, but in cereals, alleles of *Ppd-H1* and *ELF3*, which function upstream of *FT*, have been selected for breeding cultivars adapted to LD conditions (Faure et al., 2012; Turner et al., 2005). Recently, Göransson et al. (2019) found allele combinations controlling early maturation in spring barley that may enable further northward expansion of barley production.

Cultivated strawberry (*Fragaria* × *ananassa* Duch.) is one of the crops produced in the Arctic regions (Heide, 1977), and its wild-relative woodland strawberry (*F. vesca* L.) can be found in Northern Europe at latitudes up to 70°N (Hilmarsen et al., 2017). Both species are facultative SD plants that exhibit temperature-dependent photoperiodic responses (Heide, 1977; Heide & Sønsteby, 2007; Tanino & Wang, 2008). Heide (1977) found that strawberry cultivars suitable for northern Norway exhibit stronger temperature responses than other cultivars. These cultivars were able to initiate flower buds even in continuous light at cool temperatures in both controlled climate and in the field in Tromsø (69.7°N), whereas cultivars adapted to more southern climate required day lengths shorter than a critical limit and initiated flower buds several weeks later than north-adapted cultivars in the field. Another report showed that modern cultivars initiated flower buds later in northern than in southern Norway (Oppstad et al., 2011). These cultivars likely lack the temperature response reported by Heide (1977), and they are therefore less suitable for berry production in the north. Adaptation to northern climate was also reported in black currant. Cultivar Murmanschanka originating from Kola Peninsula initiated overwintering flower buds just after mid-summer in field conditions in Ås in southern Norway, whereas in

Norwegian cultivars flower initiation occurred in shorter day lengths in August (Sønsteby et al., 2012).

Molecular studies in woodland strawberry have demonstrated that a major floral repressor *TERMINAL FLOWER1* (*FvTFL1*) mediates developmental responses to photoperiod × temperature combinations (Rantanen et al., 2015). Cool temperatures below 13°C downregulate *FvTFL1* leading to photoperiod-independent flower induction. At temperatures of 13–20°C, SDs are needed to silence *FvTFL1*, whereas high temperature prevents flower induction because of high *FvTFL1* expression level (Rantanen et al., 2015). Similar photoperiod × temperature interaction in the control of *FaTFL1* expression levels was also found in cultivated strawberry cultivar Glima (Koskela et al., 2016), one of the early cultivars studied by Heide (1977). These results suggest that the regulation of *TFL1* expression level is crucial in the adaptation to northern climate in strawberries.

Global warming affects arctic flora because some wild species are moving toward north, and because human is continuously seeking for new crop cultivars and species suitable for new growing conditions (Corlett & Westcott, 2013). Examples above highlight the ability of plants to adapt to high-latitude environments by multiple means including changes in critical photoperiod for phenological responses, changes in temperature responses, and faster responses to inductive signals. Another challenge caused by global warming is the advanced spring phenology, which increases a risk of spring frost damage in some species especially in coastal regions (Ma et al., 2018). Critical questions are whether plants are able to keep the required pace in adjusting their phenological timing and whether they can tolerate more unpredictable future conditions at high latitudes.

1.5 | Arctic light and crop quality

Several studies indicate that day length, irradiance, and spectrum all affect the quality of crops, which is commonly understood as nutritional value and the sensory quality of the food plants (Kim et al., 2017; Yang et al., 2018; Zoratti et al., 2014). Nutritional value involves the levels of nutritious primary and secondary metabolites present in food plants, and sensory quality includes appearance, taste, and texture. Plant crops produce a range of secondary metabolites like terpenes, phenolics, vitamins, carotenoids, and glucosinolates associated with stress signaling and pathogens defense. Several of these compounds also possess positive effects on human health (Poiroux-Gonord et al., 2010). Both the genetic background and the surrounding environmental factors together determine the accumulation of these compounds.

A number of studies have indicated that the biosynthesis and regulation of primary and secondary metabolites is affected by high latitude light conditions (Jaakola & Hohtola, 2010). There are several field studies established in different latitudes showing that growth location has an effect on the quality factors of berry crops, although results often vary greatly across species. Long-term field studies with currant species (*Ribes* spp.) and sea buckthorn (*Hippophae rhamnoides*)

varieties growing in the north (68° 02'N) or south (60° 23'N) Finland, for example, showed contradictory results on accumulation of phenolic compounds, sugars, organic acids, or vitamin C (Yang et al., 2013; Zheng et al., 2012; Zheng, Kallio, & Yang, 2009; Zheng, Yang, et al., 2009). In red, green, and white currants, 10%–19% higher levels of phenolic compounds were detected in northern growth place, whereas black currants had lower levels of phenolic compounds in the northern locations (Yang et al., 2013; Zheng et al., 2012). Field studies with wild *Vaccinium* berries have shown a trend of higher anthocyanin levels toward Northern growth locations (Åkerström et al., 2010; Lätti et al., 2008, 2010), and sea buckthorn varieties had markedly higher proanthocyanidin levels at Northern growth locations (Yang et al., 2016; Zheng et al., 2012). Strawberries grown at different latitudes in Europe from Norway (63° 51'N) to Italy (43° 31'N) had more dry matter, and higher contents of soluble solids and titratable acids at high latitudes (Krüger et al., 2012). However, in spite of the detected correlations in accumulation of compounds with weather conditions at different locations, it is difficult to distinguish the effect of light conditions from the other environmental factors in field studies.

Controlled studies have provided more explicit information of the effect of the specific light conditions, associated to Arctic, on the quality of crop plants. It appears that longer day length has a positive effect on accumulation of flavonoids, whereas other phenolic compounds, ascorbic acid and sugars, have shown variable results. In red raspberry (*Rubus idaeus* L.), the effect of day length on the content of secondary metabolites was studied under controlled growth conditions (Mazur et al., 2014). The results showed that LDs (22/2 h light/dark) during fruit growth and maturation significantly increased the content of ascorbic acid, total phenols, and the organic acids such as malic acid, quinic acid, and ellagic acids compared to short day (10 h light, 14 h dark) conditions. At the same time, the content of sucrose and sugar-acid ratio were reduced by the LD treatments. The result of Mazur et al. (2014) indicated that photoperiodic mechanisms, rather than the received light energy per day, caused the observed differences. In another study on black currants, accumulation of anthocyanins and flavonols increased under natural LD conditions, while under identical light energy conditions, photoperiod had little or no effect on the concentration of phenolic compounds (Woznicki et al., 2016). The levels of delphinidin, peonidin, and petunidin type anthocyanins were higher in bilberries grown under 24 h of light compared with 12 h (Uleberg et al., 2012). The day length did not affect other measured compounds, such as phenolic acids, flavan-3-ols, ascorbic acid, or sugars markedly. Also in sweet potato leaves, the contents of anthocyanin, catechins, flavonols, hydroxycinnamic acids, and hydroxybenzoic acids increased dramatically when exposed to a LD photoperiod (Carvalho et al., 2010). However, LD length seems not favor accumulation of glucosinolates in *Brassica* species. Broccoli (*Brassica oleracea* L. var. *italica*) grown under controlled conditions as well as in latitudinal studies under 24 h light showed a negative effect on the accumulation of glucosinolates, flavonols, and ascorbic acid (Steindal et al., 2013). Similarly, in kale (*Brassica oleracea* L. var. *acephala*) the content of indolic glucosinolates was higher at SDs as compared to LDs (Steindal, Rødven, et al., 2015). In

Brassica species growing in 24-h photoperiod, there appears to be a disruption in circadian accumulation of glucosinolates, with lower levels found in the absence of distinct dark periods at night (Steindal, Rødven, et al., 2015). In perennial grasses, which are the most cultivated crops at high latitudes, a controlled LD treatment (24 h) increased the levels of water-soluble carbohydrates compared to 18 h day light in timothy (*Phleum pratense*) cultivars (Nordheim-Viken et al., 2009). The protein content in timothy samples was however slightly lower under the LD treatment.

Light spectrum has also shown to affect the quality of plants. The light-emitting diode (LED) systems, which have become increasingly affordable and common in greenhouse production, offer good opportunities to study the effect of light wave lengths on the growth and quality of food plants. Several studies have been performed using monochromatic LED light treatments for studying the effect of blue and/or red light on the accumulation of secondary metabolites (reviewed by Landi et al., 2020). This suggests that the arctic light conditions, which comprises prolonged period of shift toward red and far-red light, might have a positive effect on accumulation of anthocyanins and other phenolic compounds in the high latitude. This will be interesting to test across a wide range of species, as even small subtle changes in light quality may affect metabolism distinctly in even closely related cultivars/species (Samuolienė et al., 2019).

One aspect that has gotten very little attention is the generally lower level of UV-B radiation in the high latitudes due to the lower solar elevation. The ratio between UV-B and PAR decreases at high latitudes because UV-B must pass a longer path through the ozone layer when the solar angle is lower (Paul & Gwynn-Jones, 2003). Zoratti et al. (2014) showed that under clear sky mid-day conditions, UV-B level was threefold lower in Tromsø, Norway (latitude 69°N), compared to Trentino, Italy (46°N). It is well documented that UV-B through UV8 photoreceptor induces the biosynthesis of phenolic acids and flavonoids (Jenkins, 2009, 2017). As some studies have indicated even higher levels of phenolic compounds in plants growing at high latitudes, it is not clear if the lower temperatures or the longer day length compensates the lower UV-B irradiance in the arctic growth conditions. It has been shown in field studies that growth sites with higher irradiance, i.e. open areas, are associated with higher sugar, flavonoids, and hydroxycinnamic acids in wild bilberries (Mikulic-Petkovsek et al., 2015; Vaneková et al., 2020).

At high latitudes, new production systems like high tunnels are increasingly being used to both extend the season and protect the plants, especially in production of high value crops like berries. The plastics used in tunnels, however, filter some of the light and often reduce relative proportion of UV light, which may affect some of the crop quality aspects, like secondary metabolites induced by UV light. In raspberry fruit produced in Southeastern United States (41° 12'N), cyanidin-3-glucoside and the carotenoids alpha-carotene, beta-carotene, lutein, and zeaxanthin were higher in field compared with tunnel production, while total anthocyanins and tocopherols were unaffected (Bradish et al., 2015). In Helsinki (60°13'N), however, Palonen et al. (2017) did not find significant differences in the content of total phenolics between tunnel and field grown raspberries. Since the UV

irradiation is much lower at high latitude due to low solar elevation, the effect of tunnel on secondary metabolism is likely to be smaller than in the south.

Altogether, our understanding on the role of light conditions on the quality factors of the crop plants is still limited. Even closely related plant species can react differently to different light conditions (Mølmann et al., 2020; Steindal, Johansen, et al., 2015), and light \times temperature interaction has even higher effect on quality factors (Johansen et al., 2017; Steindal et al., 2013). More detailed studies are needed to clarify the role of proportional differences in the light spectrum in relation to interaction with light intensity, day length, temperature, humidity, and other factors affecting the biosynthesis of key compounds and the overall quality of the crop plants.

2 | CONCLUSIONS

Along with predicted increase of temperatures because of global warming, earlier snow melt and ground thaw in spring will give a longer Arctic growth season, especially in May/June when light conditions are most optimal during the midnight sun period. The very long daily photosynthetic light periods may allow for more rapid growth and development in crop production at high latitudes with reduced risks for autumn frosts, and enable introduction of species with warmer temperature requirements. However, despite the potential increase of biomass in many plant species, increased temperatures can also introduce new challenges in crop production at higher latitudes, with more susceptibility for plant disease, spring frosts, growth-related injuries, and reduced crop quality. Therefore, gaining a deeper understanding on the mechanisms how crop plants respond to light \times temperature interaction is utmost important, especially relating to the unique combination of Arctic light conditions and high temperatures. Furthermore, advances in how plants and crop plants integrate different light signals of irradiance, wavelength spectrum, and photoperiod will aid in the selection and breeding of future crop plants for Arctic and sub-Arctic latitudes in the future.

ACKNOWLEDGMENTS

This work was financially supported by NordPlant (NordForsk grant no. 84597), The Research Council of Norway (NFR – Bionær grant no. 296397) and Grofondet AS (Grant no. 190028).

AUTHOR CONTRIBUTIONS

All authors were involved in planning and writing the manuscript. Jørgen A. B. Mølmann and Amos Samkumar created and adapted the Figures 1–4.

DATA AVAILABILITY STATEMENT

The climate data presented were derived from the following resources available in the public domain: <https://lmt.nibio.no/> (Landbruks Meteorologisk Tjeneste - The Norwegian Agricultural Meteorology Service).

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REFERENCES

- Åkerström, A., Jaakola, L., Bång, U. & Jäderlund, A. (2010) Effects of latitude-related factors and geographical origin on anthocyanidin concentrations in fruits of *Vaccinium myrtillus* L. (bilberries). *Journal of Agricultural and Food Chemistry*, 58, 11939–11945.
- Andres, F. & Coupland, G. (2012) The genetic basis of flowering responses to seasonal cues. *Nature Reviews. Genetics*, 13, 627–639.
- Baker, B. & Jung, G.A. (1968) Effect of environmental conditions on the growth of four perennial grasses. I. Response to controlled temperature. *Agronomy Journal*, 60, 155–158.
- Bertrand, A., Tremblay, G.F., Pelletier, S., Castonguay, Y. & Bélanger, G. (2008) Yield and nutritive value of timothy as affected by temperature, photoperiod and time of harvest. *Grass and Forage Science*, 63, 421–432.
- Björn, L.O. (2015) Photoreceptive proteins and their evolution. In: *Photobiology: the science of light and life*. New York: Springer, pp. 169–176.
- Böhlenius, H., Huang, T., Charbonnel-Campaa, L., Brunner, A.M., Jansson, S., Strauss, S.H. et al. (2006) CO/FT regulatory module controls timing of flowering and seasonal growth cessation in trees. *Science*, 312, 1040–1043.
- Bootsma, A. (1984) Forage crop maturity zonation in the Atlantic region using growing degree-days. *Canadian Journal of Plant Science*, 64, 329–338.
- Bradish, C.M., Yousef, G.G., Ma, G.Y., Perkins-Veazie, P. & Fernandez, G.E. (2015) Anthocyanin, carotenoid, tocopherol, and ellagitannin content of red raspberry cultivars grown under field or high tunnel cultivation in the southeastern United States. *American Society for Horticultural Science*, 140, 163–171.
- Carvalho, I.S., Cavacoa, T., Carvalho, L.M. & Duque, P. (2010) Effect of photoperiod on flavonoid pathway activity in sweet potato (*Ipomoea batatas* [L.] Lam.) leaves. *Food Chemistry*, 118, 384–390.
- Clapham, D.H., Dormling, I., Ekberg, I., Eriksson, G., Qamaruddin, M. & Vince-Prue, D. (1998) Latitudinal cline of requirement for far-red light for the photoperiodic control of budset and extension growth in *Picea abies* (Norway spruce). *Physiologia Plantarum*, 102, 71–78.
- Corlett, R.T. & Westcott, D.A. (2013) Will plant movements keep up with climate change? *Trends in Ecology and Evolution*, 28, 482–488.
- Faure, S., Turner, A.S., Gruszka, D., Christodoulou, V., Davis, S.J., von Korff, M. et al. (2012) Mutation at the circadian clock gene EARLY MATURITY 8 adapts domesticated barley (*Hordeum vulgare*) to short growing seasons. *Proceedings of the National Academy of Sciences of the United States of America*, 109, 8328–8333.
- Gates, D.M. (1980) *Biophysical ecology*. New York: Springer-Verlag, pp. 96–147.
- Göransson, M., Hallsson, J.H., Lillemo, M., Orabi, J., Backes, G., Jahoor, A. et al. (2019) Identification of ideal allele combinations for the adaptation of spring barley to northern latitudes. *Frontiers in Plant Science*, 10, 542.
- Hanssen-Bauer, I., Førland, E.J., Haddeland, I., Hisdal, H., Mayer, S., Nesje, A. et al. (2015) Klima i Norge 2100. Kunnskapsgrunnlag for klimatilpasning oppdatert i 2015. M-406, KSS rapport, 2(2015), 1–203 (in Norwegian).
- Hårdh, J.E., Persson, A.R. & Ottosson, L. (1977) Quality of vegetables cultivated at different latitudes in Scandinavia. *Acta Agriculturae Scandinavica*, 27, 81–96.
- Hay, R.K.M. & Pedersen, K. (1986) Influence of long photoperiods on the growth of timothy (*Phleum pratense* L.) varieties from different latitudes in northern Europe. *Grass and Forage Science*, 41, 311–317.

- Haydon, M.J., Mielczarek, O., Robertson, F.C., Hubbard, K.E. & Webb, A.A. R. (2013) Photosynthetic entrainment of the *Arabidopsis thaliana* circadian clock. *Nature*, 502, 689–693.
- Heide, O.M. (1977) Photoperiod and temperature interactions in growth and flowering of strawberry. *Physiologia Plantarum*, 40, 21–26.
- Heide, O.M. (1982) Effects of photoperiod and temperature on growth and flowering in norwegian and british timothy cultivars (*Phleum pratense* L.). *Acta Agriculturae Scandinavica*, 32, 241–252.
- Heide, O.M. (1985) Physiological aspects of climatic adaptation in plants with special reference to high-latitude environments. In: Kauren, Å., Junntila, O. & Nilsen, J. (Eds.) *Plant production in the north*. Oslo: Norwegian University Press, pp. 1–22.
- Heide, O.M. (1994) Control of flowering and reproduction in temperate grasses. *The New Phytologist*, 128, 347–362.
- Heide, O.M., Hay, R.K.M. & Bøgerød, H. (1985) Specific daylength effects on leaf growth and dry matter production in high-latitude grasses. *Annals of Botany*, 55, 579–586.
- Heide, O.M. & Sønsteby, A. (2007) Interactions of temperature and photoperiod in the control of flowering of latitudinal and altitudinal populations of wild strawberry (*Fragaria vesca*). *Physiologia Plantarum*, 130, 280–289.
- Hilmarsson, H.S., Hytönen, T., Isobe, S., Göransson, M., Toivainen, T. & Hallsson, J.H. (2017) Population genetic analysis of a global collection of *Fragaria vesca* using microsatellite markers. *PLoS One*, 12, e0183384.
- Hoecker, U. (2017) The activities of the E3 ubiquitin ligase COP1/SPA, a key repressor in light signaling. *Current Opinion in Plant Biology*, 37, 63–69.
- Hüner, N.P.A., Bode, R., Dahal, K., Hollis, L., Rosso, D., Krol, M. et al. (2012) Chloroplast redox imbalance governs phenotypic plasticity: the “grand design of photosynthesis” revisited. *Frontiers in Plant Science*, 3, 255. <https://doi.org/10.3389/fpls.2012.00255>.
- Hüner, N.P.A., Dahal, K., Kurepin, L., Savitch, L., Singh, J., Ivanov, A.G. et al. (2014) Potential for increased photosynthetic performance and crop productivity in response to climate change: role of CBFs and gibberellic acid. *Frontiers in Chemistry*, 2, 18. <https://doi.org/10.3389/fchem.2014.00018>.
- Inada, K. & Yabumoto, Y. (1989) Effects of light quality, daylength and periodic temperature variation on the growth of lettuce and radish plants. *Japanese Journal of Crop Science*, 58, 689–694.
- Jaakola, L. & Hohtola, A. (2010) Effect of latitude on flavonoid biosynthesis in plants. *Plant, Cell and Environment*, 33, 1239–1247.
- Jenkins, G.I. (2009) Signal transduction in responses to UV-B radiation. *Annual Review of Plant Biology*, 60, 407–431.
- Jenkins, G.I. (2017) Photomorphogenic responses to ultraviolet-B light. *Plant, Cell and Environment*, 40, 2544–2557.
- Jiao, Y., Lau, O.S. & Deng, X.W. (2007) Light-regulated transcriptional networks in higher plants. *Nature Reviews Genetics*, 8, 217–228.
- Johansen, T.J., Mølmann, J.A.B., Bengtsson, G.B., Schreiner, M., Velasco, P., Hykkerud, A.L. et al. (2017) Temperature and light conditions at different latitudes affect sensory quality of broccoli florets (*Brassica oleracea* L. var. *italica*). *Journal of the Science of Food and Agriculture*, 97, 3500–3508.
- Junntila, O. (1980) Effect of photoperiod and temperature on apical growth cessation in two ecotypes of *Salix* and *Betula*. *Physiologia Plantarum*, 48, 347–352.
- Junntila, O., Svenning, M.M. & Solheim, B. (2006) Effects of temperature and photoperiod on frost resistance of white clover (*Trifolium repens*) ecotypes. *Physiologia Plantarum*, 79, 435–438.
- Kim, J.A., Kim, H.S., Choi, S.H., Jang, J.Y., Jeong, M.J. & Lee, S.I. (2017) The importance of the circadian clock in regulating plant metabolism. *International Journal of Molecular Sciences*, 18, 2680.
- Koskela, E.A., Sønsteby, A., Flachowsky, H., Heide, O.M., Hanke, M.V., Elomaa, P. et al. (2016) *TERMINAL FLOWER1* is a breeding target for a novel everbearing trait and tailored flowering responses in cultivated strawberry (*Fragaria × ananassa* Duch.). *Plant Biotechnology Journal*, 14, 1852–1861.
- Krüger, E., Josuttis, M., Nestby, R., Toldam-Andersen, T.B., Carlen, C. & Mezzetti, B. (2012) Influence of growing conditions at different latitudes of Europe on strawberry growth performance, yield and quality. *Journal of Berry Research*, 2, 143–157.
- Landi, M., Zivac, M., Sytar, O., Brestic, M. & Allakhverdiev, S.I. (2020) Plasticity of photosynthetic processes and the accumulation of secondary metabolites in plants in response to monochromatic light environments: a review. *Biochimica et Biophysica Acta - Bioenergetics*, 1861, 148131.
- Lätti, A.K., Jaakola, L., Riihinen, K.R. & Kainulainen, P.S. (2010) Anthocyanin and flavonol variation in bog bilberries (*Vaccinium uliginosum* L.) in Finland. *Journal of Agricultural and Food Chemistry*, 58, 427–433.
- Lätti, A.K., Riihinen, K.R. & Kainulainen, P.S. (2008) Analysis of anthocyanin variation in wild populations of bilberry (*Vaccinium myrtillus* L.) in Finland. *Journal of Agricultural and Food Chemistry*, 56, 190–196.
- Ma, Q., Huang, J., Hänninen, H. & Berninger, F. (2018) Divergent trends in the risk of spring frost damage to trees in Europe with recent warming. *Global Change Biology*, 25, 351–360.
- Mawson, B.T., Svoboda, J. & Cummins, R.W. (1986) Thermal acclimation of photosynthesis by the arctic plant *Saxifraga cernua*. *Canadian Journal of Botany*, 64, 71–76.
- Mazur, S.P., Sønsteby, A., Wold, A.B., Foito, A., Freitag, S., Verrall, S. et al. (2014) Post-flowering photoperiod has marked effects on fruit chemical composition in red raspberry (*Rubus idaeus*). *The Annals of Applied Biology*, 165, 454–465.
- McKenzie, J.S., Weiser, C.J. & Burke, M.J. (1974) Effects of red and far red light on the initiation of cold acclimation in *Cornus stolonifera* Michx. *Plant Physiology*, 53, 783–789.
- Mikulic-Petkovsek, M., Schmitzer, V., Slatnar, A., Stampar, F. & Veberic, R. (2015) A comparison of fruit quality parameters of wild bilberry (*Vaccinium myrtillus* L.) growing at different locations. *Journal of the Science of Food and Agriculture*, 95, 776–785.
- Milford, G.F.J. & Lenton, J.R. (1976) Effect of photoperiod on growth of sugar beet. *Annals of Botany*, 40, 1309–13015.
- Mølmann, J.A., Junntila, O., Johnsen, Ø. & Olsen, J.E. (2006) Effects of red, far-red and blue light maintaining growth in latitudinal populations of Norway spruce (*Picea abies*). *Plant, Cell & Environment*, 29, 166–172.
- Mølmann, J.A.B., Hagen, S.F., Bengtsson, G.B. & Johansen, T.J. (2018) Influence of high latitude light conditions on sensory quality and contents of health and sensory-related compounds in swede roots (*Brassica napus* L. ssp. *rapifera* Metzg.). *Journal of the Science of Food and Agriculture*, 98, 1117–1123.
- Mølmann, J.A.B., Hansen, E. & Johansen, T.J. (2020) 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. *Journal of the Science of Food and Agriculture*, 101, 2422–2427.
- Navarro, C., Abelenda, J.A., Cruz-Oró, E., Cuéllar, C.A., Tamaki, S., Silva, J. et al. (2011) Control of flowering and storage organ formation in potato by FLOWERING LOCUS T. *Nature*, 478, 119–122.
- Nilsen, J. (1985) Light climate in northern areas. In: Kaurin, Å., Junntila, O. & Nilsen, J. (Eds.) *Plant production in the north*. Oslo: Norwegian University Press, pp. 62–72.
- Nordheim-Viken, H., Volden, H. & Jørgensen, M. (2009) Effects of maturity stage, temperature and photoperiod on growth and nutritive value of timothy (*Phleum pratense* L.). *Animal Feed Science and Technology*, 152, 204–218.
- Obu, J., Westermann, S., Bartsch, A., Berdnikov, N., Christiansen, H.H., Dashtseren, A. et al. (2019) Northern hemisphere permafrost map based on TOP modelling for 2000–2016 at 1 km² scale. *Earth Science Reviews*, 193, 299–316.
- Olsen, J.E., Junntila, O., Nilsen, J., Eriksson, M.E., Martinussen, I., Olsson, O. et al. (1997) Ectopic expression of oat phytochrome a in hybrid aspen

- changes critical daylength for growth and prevents cold acclimatization. *The Plant Journal*, 12, 1339–1350.
- Oppstad, N., Sønsteby, A., Myrheim, U. & Heide, O.M. (2011) Seasonal timing of floral initiation in strawberry: effects of cultivar and geographic location. *Scientia Horticulturae*, 129, 127–134.
- Palonen, P., Pinomaa, A. & Tommila, T. (2017) The influence of high tunnel on yield and berry quality in three florican raspberry cultivars. *Scientia Horticulturae*, 214, 180–186.
- Paul, N.D. & Gwynn-Jones, D. (2003) Ecological roles of solar UV radiation: towards an integrated approach. *Trends in Ecology & Evolution*, 18, 48–55.
- Poiroux-Gonord, F., Bidel, L.P.R., Fanciullino, A.-L., Gautier, H., Lauri-Lopez, F. & Urban, L. (2010) Health benefits of vitamins and secondary metabolites of fruits and vegetables and prospects to increase their concentrations by agronomic approaches. *Journal of Agricultural and Food Chemistry*, 58, 12065–12082.
- Rantanen, M., Kurokura, T., Jiang, P., Mouhu, K. & Hytönen, T. (2015) Strawberry homologue of TERMINAL FLOWER1 integrates photoperiod and temperature signals to inhibit flowering. *The Plant Journal*, 82, 163–173.
- Salisbury, F.B. (1981) Twilight effect: initiating dark measurement in photoperiodism of xanthium. *Plant Physiology*, 67, 1230–1238.
- Samuolienė, G., Brazaitytė, A., Viršilė, A., Miliauskienė, J., Vastakaitė-Kairienė, V. & Duchovskis, P. (2019) Nutrient levels in *Brassicaceae* microgreens increase under tailored light-emitting diode spectra. *Frontiers in Plant Science*, 10, 1475.
- Semikhatova, O.A., Gerasimenko, T.V. & Ivanova, T.I. (1992) Photosynthesis, respiration, and growth of plants in the soviet Arctic. In: Chapin, F.S., III, Jefferies, R.L., Reynolds, J.F., Shaver, G.R. & Svoboda, J. (Eds.) *Arctic ecosystems in a changing climate*. San Diego: Academic Press, pp. 169–192.
- Simonsen, Ø. (1985) Herbage breeding in northern areas. In: Kaurin, Å., Junntila, O. & Nilsen, J. (Eds.) *Plant production in the north*. Oslo: Norwegian University Press, pp. 277–295.
- Smith, H. (2000) Phytochromes and light signal perception by plants—an emerging synthesis. *Nature*, 407, 585–591.
- Solhaug, K.A. (1991) Long day stimulation of dry matter production in *Poa alpina* along a latitudinal gradient in Norway. *Holarctic Ecology*, 14, 161–168.
- Sønsteby, A., Oppstad, N. & Heide, O.M. (2012) Effects of summer temperature on growth and flowering in six black currant cultivars (*Ribes nigrum* L.). *Journal of Horticultural Science*, 87, 157–164.
- Sørensen TJ (1941) Temperature relations and phenology of the Northeast Greenland flowering plants. Medd Grøn, Vol. 125, C.A. Reitzel, Copenhagen.
- Steindal, A.L.H., Johansen, T.J., Bengtsson, G.B., Hagen, S.F. & Mølmann, J. A.B. (2015) Impact of pre-harvest light spectral properties on health- and sensory-related compounds in broccoli florets. *Journal of the Science of Food and Agriculture*, 96, 1974–1981.
- Steindal, A.L.H., Mølmann, J., Bengtsson, G.B. & Johansen, T.J. (2013) Influence of day length and temperature on the content of health-related compounds in broccoli (*Brassica oleracea* L. var. *italica*). *Journal of Agricultural and Food Chemistry*, 61, 10779–10786.
- Steindal, A.L.H., Rødven, R., Hansen, E. & Mølmann, J. (2015) Effects of photoperiod, growth temperature and cold acclimatization on glucosinolates, sugars and fatty acids in kale. *Food Chemistry*, 174, 44–51.
- Tanino, K.K., Bandara, M.S., Krieger, K., Ward, T., Ito, B., Ozawa, S. et al. (2006) Northern vigour® in strawberry crowns. *Acta Horticulturae*, 708, 225–230.
- Tanino, K.K. & Wang, R. (2008) Modeling chilling requirement and diurnal temperature differences on flowering and yield performance in strawberry crown production. *Horticultural Science*, 43, 2060–2065.
- Turner, A., Beales, J., Faure, S., Dunford, R.P. & Laurie, D.A. (2005) The pseudo response regulator Ppd-H1 provides adaptation to photoperiod in barley. *Science*, 310, 1031–1034.
- Uleberg, E., Rohloff, J., Jaakola, L., Tröst, K., Junntila, O., Häggman, H. et al. (2012) Effects of temperature and photoperiod on yield and chemical composition of northern and southern clones of bilberry (*Vaccinium myrtillus* L.). *Journal of Agricultural and Food Chemistry*, 60, 10406–10414.
- Uleberg, E.I., Hanssen-Bauer, I., van Oort, B. & Dalmannsdottir, S. (2014) Impact of climate change on agriculture in northern Norway and potential strategies for adaptation. *Climatic Change*, 122, 27–39.
- Vaneková, Z., Vanek, M., Škvarenina, J. & Nagy, M. (2020) The influence of local habitat and microclimate on the levels of secondary metabolites in Slovak bilberry (*Vaccinium myrtillus* L.). *Plants*, 9, 436.
- Woznicki, T.L., Aaby, K., Sønsteby, A., Heide, O.M., Wold, A.B. & Remberg, S.F. (2016) Influence of controlled postflowering temperature and day length on individual phenolic compounds in four black currant cultivars. *Journal of Agricultural and Food Chemistry*, 64, 752–761.
- Wu, Z., Skjelvåg, S. & Baadshaug, O.H. (2004) Quantification of photoperiodic effects on growth of *Phleum pratense*. *Annals of Botany*, 94, 533–543.
- Yang, B., Zheng, J., Laaksonen, O., Tahvonen, R. & Kallio, H. (2013) Effects of latitude and weather conditions on phenolic compounds in currant (*Ribes* spp.) cultivars. *Journal of Agricultural and Food Chemistry*, 61, 3517–3532.
- Yang, L., Wen, K.-S., Ruan, X., Zhao, Y.-X., Wei, F. & Wang, Q. (2018) Response of plant secondary metabolites to environmental factors. *Molecules*, 23, 762. <https://doi.org/10.3390/molecules23040762>.
- Yang, W., Laaksonen, O., Kallio, H. & Yang, B. (2016) Proanthocyanidins in sea buckthorn (*Hippophaë rhamnoides* L.) berries of different origins with special reference to the influence of genetic background and growth location. *Journal of Agricultural and Food Chemistry*, 64, 1274–1282.
- Zheng, J., Kallio, H. & Yang, B. (2009) Effects of latitude and weather conditions on sugars, fruit acids, and ascorbic acid in currant (*Ribes* sp.) cultivars. *Journal of the Science of Food and Agriculture*, 89, 2011–2023.
- Zheng, J., Yang, B., Ruusunen, V., Laaksonen, O., Tahvonen, R., Hellsten, J. et al. (2012) Compositional differences of phenolic compounds between black currant (*Ribes nigrum* L.) cultivars and their response to latitude and weather conditions. *Journal of Agricultural and Food Chemistry*, 60, 6581–6593.
- Zheng, J., Yang, B., Tuomasjukka, S., Ou, S. & Kallio, H. (2009) Effects of latitude and weather conditions on contents of sugars, fruit acids, and ascorbic acid in black currant (*Ribes nigrum* L.) juice. *Journal of Agricultural and Food Chemistry*, 57, 2977–2987.
- Zoratti, L., Karppinen, K., Luengo Escobar, A., Häggman, H. & Jaakola, L. (2014) Light-controlled flavonoid biosynthesis in fruits. *Frontiers in Plant Science*, 5, 534.

How to cite this article: Mølmann JAB, Dalmannsdottir S, Hykkerud AL, Hytönen T, Samkumar A, Jaakola L. Influence of Arctic light conditions on crop production and quality. *Physiologia Plantarum*. 2021;1–10. <https://doi.org/10.1111/ppl.13418>