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# Plants under Continuous Light: A Review

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## ABSTRACT

In this review an attempt has been made to analyze the results of the studies that explored the changes in the growth and development of plants exposed to continuous light published since the 1930s, including papers that are available in Russian only. Potential benefits of using a 24-h photoperiod for the production of greenhouse crops, transplant production in closed controlled environment systems and the culture of plants in controlled ecological life support systems are reviewed. Continuous lighting is shown to be a useful tool for speeding up the selection of crops. The mechanisms involved in a plant's response to continuous light and causes of negative effects of continuous light (foliar chlorosis, limited or reduced plant growth and productivity) are discussed. Plant response to continuous light depends on plant tolerance and can be modified by alterations in temperature, light intensity, $CO_2$ level, humidity, mineral nutrition and other environmental factors.

**Keywords:** 24-h photoperiod, growth, development, photosynthesis, chlorosis

**Abbreviations: CAT**, catalase; **CELSS**, controlled ecological life support systems; **chl**, chlorophyll; **DM**, dry matter; **LAR**, leaf area ratio; **LDP**, long-day plant; **NAR**, net assimilation rate; **NDP**, neutral-day plant; **PAR**, photosynthetically active radiation; **POD**, peroxidase; **PPF**, photosynthetic photon flux; **SDP**, short-day plant; **SLA**, specific leaf area; **SOD**, superoxide dismutase; **SPS**, sucrose phosphate synthase

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## INTRODUCTION

Light as an energy source for plant life is known to affect plants dually. It affects photosynthetic rate and assimilate accumulation, thereby playing a substrate role, but also controls plant growth and development, in that way playing a regulatory role. While plant growth in short-day (SD) and long-day (LD) conditions is generally well studied and has been reviewed recently by Adams and Langton (2005), less is known about the long-term impact of continuous light on plant growth and development, when many plant circadian rhythms are disrupted. Studies of plant growth and development under continuous light are of current importance for the production of greenhouse crops, where daily timing of supplementary lighting can be manipulated to maximize plant response or to minimize the heating costs by spreading the daily light integral from artificial sources over as many hours as possible. Growing plants under continuous light is a way of producing crops economically in controlled environment growth rooms. With extension to continuous radiation, savings possibility could be realized by decreasing the number of light fixtures per unit area and by prolonging useful lamp life (no on/off deterioration). Transplant production in closed controlled environment systems (CCES) with artificial lighting, which have several potential benefits compared with conventional systems also requires knowledge of plant response to continuous light. In the culture of plants in controlled ecological life support systems (CELSS) in long duration space bases, it is essential to maximize plant growth rates or production of edible biomass per unit area per unit time. Limitations for plant growth in space include energy needed to produce light for photosynthesis. In an effort to deal with the low energy constraints during extended space missions, the use of low photosynthetic photon flux (PPF) has to be a viable alternative. One way to increase the daily total PPF is to extend the daily light period and/or provide continuous (24 h) lighting (Rowell *et al*. 1999). Wheat (*Triticum aestivum* L.), potatoes (*Solanum tuberosum* L.), soybeans (*Glycine max* (L.) Merr.), lettuce (*Lactuca sativa* L.), tomato (*Solanum lycopersicum* L.), peanut (*Arachis hypogaea* L.), rice (*Oryza sativa* L.), barley (*Hordeum vulgare* L.), oats (*Avena sativa* L.), rye (*Secale cereale* L.), sorghum (*Sorghum bicolor* (L.) Moench.), quinoa (*Chenopodium quinoa* Willd.) and other crops have been under investigation for use in the NASA's CELSS/Advanced Life Support (ALS) program as a food source for extended space missions. Continuous lighting can be a very useful tool for speeding

**Received: 29 April, 2010. Accepted: 20 October, 2010.**

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up selection of crops. Accelerated development of some plant species under continuous lighting allows breeders shortening of the generation cycle having more generations a year. It also permits breeders to have closer ripening terms of early- and late-season varieties and varieties with different photoperiodic sensitivity, which is important in growing of hybrid material. Besides, it decreases the dispersion of particular plant features (Lisovskij and Dolgushev 1986). Studying plant responses to continuous light may provide us with better understanding of plant adaptations in the Arctic under conditions of polar day with a 24-h photoperiod. Thus, according to Hay (1990) there have been two reasons for the sustained interest in the influence of daylength extension on growth. On the one hand, pasture grass breeders have become interested in the adaptation shown by commercially important species to the diverse combinations of temperature and photoperiod experienced in maritime and continental Europe. A major aim of this work has been to increase spring and autumn production without sacrificing winter hardiness. On the other hand, plant selection and breeding in Scandinavia has led to the development of named varieties of several grass species which are adapted to growing seasons near the Arctic Circle (continuous illumination and cool temperature) (Simonsen 1985).

This paper is focused on findings achieved in various experiments where plants were exposed to continuous light and summarizes the knowledge about the impact of continuous light on plant development, photosynthesis and growth, yield, and development of physiological disorders.

## PLANT DEVELOPMENT UNDER CONTINUOUS LIGHT

There are reports in the literature of continuous light both increasing plant developmental rate and inhibiting development. In most of long-day plants (LDP) continuous light accelerated the reproductive cycle, while short-day plants (SDP) usually did not respond in such a way. Thus, continuous light was shown to increase the developmental rate in 30 spring wheat (LDP) cultivars of different geographical origin (Zhukov and Romanovskaja 1980), barley (LDP), radish (*Raphanus sativus* L.) (LDP) (Lisovskij and Dolgushev 1986; Moshkov 1987), LD and neutral day (ND) pea varieties (*Pisum sativum* L.) (Kornilov 1968; Berry and Aitken 1979; Lisovskij and Dolgushev 1986). For LD legume chickpea (*Cicer arietinum* L.), supplemental lighting was recommended under Indian conditions in order to provide continuous illumination, which greatly reduces the vegetation period and allows breeders obtaining four generations of chickpea a year (Sethi *et al.* 1981). In contrast, SD legume crop peanut was found to be relatively insensible of photoperiod as regards to the time to the appearance of first flower, while continuous light slightly increased the number of leaves produced per plant, although flower production was substantially enhanced among plants grown under the shorter (12 h) light period (Rowell *et al.* 1999). Alfalfa (*Medicago sativa* L.) is a typical LD perennial plant and in middle latitudes it often does not produce seeds on the first year, which means it takes 3-5 years to obtain seeds of the 2nd or 3rd generation. However, illumination by continuous light allowed obtaining mature alfalfa seeds in 90 days from sowing (Lisovskij and Dolgushev 1986). Rapid growth of alfalfa under continuous light was accompanied by enhanced tillering and formation of a great number of inflorescences without simultaneous growth retarding as it usually occurs in annual plants. Continuous light also turned out to be a useful tool for the breeders of such LDP as oilseed rape (*Brassica napus* L.) and yellow rocket (*Barbarea vulgaris* R.Br.) providing the possibility to obtain 3 generations of rape plants and 4 generations of yellow rocket in the winter period and ensuring more uniform material in respect of developmental rate, time of flowering, leafiness, etc. compared to 14-16-h photoperiod (Lisovskij and Dolgushev 1986). Three generations of flax (*Linum usitatissimum* L.) (LDP) a year can be also grown under continuous light providing high yields (Lisovskij and Dolgushev 1986). Continuous light is commonly used to accelerate the reproductive cycle in Arabidopsis (*Arabidopsis thaliana* (L.) Heynh.) (LDP) (Handling Arabidopsis Plants and Seeds 2004; Massa *et al.* 2007). It was assumed that the 24-hour illuminated Arabidopsis plants may not produce as much seed, having had less time to accumulate carbohydrates by vegetative growth (Massa *et al.* 2007). However, only one report was found suggesting that lower seed yields results from this treatment, and it involved 'weak mutants' (Hirono 1964).

In pot roses (*Rosa x hybrida*) (neutral-day plant (NDP)) continuous light decreased the number of days to flowering by 12% and increased the number of flowers by 34% compared to 18-h photoperiod (Pettersen *et al.* 2006, 2007). In contrast, continuous light had no influence on number of days to flowering for *Begonia* (LDP) and geranium (*Pelargonium x hortorum* Bailey) (NDP), while increased the number of buds and flowers in begonia compared to 16-h daylength (Gislerød *et al.* 1989).

The response of SDPs to continuous light is somewhat different. Thus, in millet (*Panicum miliaceum* L.) (SDP) continuous light decreased developmental rate compared to shorter photoperiods, but nevertheless a number of researchers reported that almost all tested millet cultivars flowered and produced seeds under continuous illumination when natural day was extended by supplemental lighting (Kornilov 1968; Lisovskij and Dolgushev 1986). Extension of photoperiod up to continuous light considerably extended the reproductive cycle, but increased total plant biomass and seed yield. Interestingly, continuous light extended the vegetation period of early-season cultivars compared to field conditions but shortened it in late-season cultivars, thereby reducing the difference between vegetation duration of utmost cultivars (Lisovskij and Dolgushev 1986). In contrast, early-season varieties of soybean (SDP) grown under continuous light did not demonstrate the delay in flowering compared to natural daylength (17.5 h), while the ripening was considerably (by 30-50 days) delayed in 16 out of 44 tested varieties (Davydenko *et al.* 2004).

Sunflower (*Helianthus annuus* L.) is regarded by many researchers as SDP or NDP; nevertheless, Gvozdeva (1981) observed shortening of the vegetation period of sunflower under continuous light by 3-7 days compared to 16-h photoperiod. Also Voskobojnik *et al.* (1981) concluded that SD was not necessary for normal growth and development of sunflower and photoperiods of 16 or 24-h were quite suitable, although 24-h photoperiod did not have benefits in respect of yield and energy inputs. The developmental rate of the typical SDP cotton (*Gossypium* spp.) was found to be higher under continuous light compared to SD at light intensity of 250 W m$^{-2}$ (Shul'gin 1973). Continuous lighting resulted in earlier flowering and fruiting of pepper plants (*Capsicum annuum* L.) (a moderately SDP) giving better early yields, compared with a 15-h photoperiod, while final productivity was identical for the two photoperiods (Costes and Milhet 1970). Different responses of SDPs to continuous light may be related to species biology as different species have evolved different mechanisms to respond to photoperiod (Jackson 2009) or variations of other environmental conditions, i.e. photoperiod-temperature interactions. In our research, we observed that in soybean (SDP) the development was accelerated by 24-h illumination only when daily temperature gradient was applied (Markovskaja and Sysoeva 2004). It was found also that daily short-term temperature drop may hasten plant development under continuous light. Thus, daily temperature drop to hardening temperature for 4 to 6 hours increased leaf initiation rate and lateral branching at early stages of ontogenesis in cucumber plants (*Cucumis sativus* L.) grown under continuous light (Sysoeva *et al.* 2007).

There are reports that continuous light initiated senescence earlier than shorter photoperiods, indicating accelerated development of plants. This was found to be the case by Gestel *et al.* (2005) who observed that onion plants (*Allium cepa* L.) grown in continuous light completed their growth stages about 45 days earlier than under normal field conditions. The more rapid senescence of leaves was observed in potato plants grown under 24-h photoperiod (Wheeler and Tibbitts 1987).

There are some reports in the scientific literature with the examples of the use of continuous light to accelerate trees and shrubs timing. Thus, in experiments of Hohlova *et al.* (1976) and Moshkov (1987) with black currant (*Ribes nigrum* L.) they were unable in the first year to stimulate flowering by continuous light, although plants grew vigorously and at the age of 2-2,5 months looked like 2-year-old seedlings. Later Hohlova *et al.* (1979) found a particular combination of continuous light followed by SD resulted in flowering of 70% of plants at the age of 9 months and fruiting of 58% of plants. Hohlova (1979) also observed that seedlings grown under continuous light followed by SD had compared well with 3-5-year old fruiting seedlings in the field as regards to flowering intensity, disease resistance and winter hardiness. The ability to obtain black currant flowering in the first year allowed breeders intensification of their work as usually it required 3-5 years in Siberia to estimate cultivars by their fruit quality (Lisovskij and Dolgushev 1986). Working with honeysuckle (*Lonicera edulis* Turcz. Ex Freyn), sea buckthorn (*Hippophae rhamnoides* L.) and apple trees *(Malus domestica* Borkh.) Lisovskij and Dolgushev (1986) showed that grown under continuous light for 4-6.5 months plants looked similar to 2-3-year-old field grown seedlings and were suitable for spring transplanting to permanent place. They failed to induce flowering in the first year, nevertheless plants flowered and fruited some years earlier compared to field-grown plants.

Plant response to continuous light may vary depending on the stage of plant development. Demers and Gosselin (2002) stated that although long-term use of continuous light is detrimental to tomato and sweet pepper plants, early vegetative growth and fruit production of both species can be improved by short-term use (5 to 7 weeks) of continuous lighting. Demers *et al.* (1998a) reported that continuous lighting hastened flowering of tomato plants but only during the first weeks. At the end of the experiment there was no difference between 14-h and 24-h photoperiods in the number of clusters that had reached anthesis. In experiments with pea flowering was most rapid in 24-h photoperiod, but the duration of the period from floral initiation to first flower was independent of photoperiod (Berry and Aitken 1979) suggesting that any differences in flowering between treatments arose prior to floral initiation. Many authors (Kleshnin *et al.* 1959; VNIIZH 1978; Zhukov and Romanovskaja 1980 *et al.*) believe that the most efficient is such light regime when at the early stages of ontogenesis plant development is slightly hampered by SD and then, in the period of intensive photosynthetic activity plants are provided with continuous lighting. It was shown that wheat grain yield was maximum when plants were provided with 16-18-h photoperiod during first 20-30 days followed by continuous light (Zhukov and Romanovskaja 1980; Lisovskij and Dolgushev 1986). Such lighting regime reduced radiant energy cost per grain yield by 20-30% while extending vegetation period by only 5-8 days. The most effective growing regime for barley was when 18-h photoperiod given for the first 20 days from seedling emergence was followed by continuous light (VNIIZH 1978). According to Kornilov (1968), millet is photoperiodically sensitive in the period from seedling emergence to the stage of 7-8 leaves. SD applied during the seedling emergence – paniculation period by enhancing development greatly reduced growth compared to continuous light treatment. It was suggested to apply SD for the development acceleration during shorter time, while 3-4 leaves appear and then grow millet under continuous light (Lisovskij and Dolgushev 1986). With this aim 24 cultivars of millet from 14 ecologo-geographical groups were tested. In these experiments, 16-h photoperiod during 3 weeks followed by continuous light accelerated development more than continuous light or natural daylength, but continuous light was highly competitive in respect of energy input per unit yield. It has been noted above that the best regime for black currant was a combination of continuous light followed by SD resulted in flowering of plants at the age of 9 months (Hohlova *et al.* 1979). Findings by Sato *et al.* (2009) indicated that day-extension treatments from the middle term of growth until flowering time with more than 0.7 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of far red light promoted a high production of marketable cut flowers of the *Eustoma grandiflorum* in early winter in the cool area in Japan and the effect was greatest with continuous lighting. Thus, many factors including photoperiodic sensitivity and responsiveness, precocity, developmental stage and environmental conditions affect plant developmental response to continuous light.

There are several indications of the role of continuous light spectrum in plant development. Thus, Kasajima *et al.* (2007) investigated the developmental rate of wheat (a Japanese spring wheat var. Norin 61 and a winter wheat var. Shun-yo) under continuous light of eight different qualities obtained by combining three out of four different kinds of fluorescent lamps (white, blue, purplish red and ultraviolet-A) at a constant temperature of 20°C. Results suggested that green and red lights play important roles in the regulation of the developmental rate having a promotive effect, independent of photoperiodism and vernalisation. This research aimed to accelerate heading, which shortens the generation cycle and improves the efficiency of the crossing. Apple trees grown under continuous light developed faster when supplemental red lighting was used (Isaeva 1978), while accelerated development of cucumber plants was observed when they were treated by supplemental blue light (L'vova 1978). Under continuous light, longer period of natural lighting in combination with shorter period of fluorescent lighting resulted in considerably faster generative development of vetch (*Vicia* spp.) plants (Rzhanova 1978). The great effect of light quality for continuous illuminating at 'night' on floral initiation of wild strawberry (*Fragaria chiloensis* L.) grown under a 24-h photoperiod was shown by Yanagi *et al.* (2006).

## PLANT GROWTH AND PRODUCTIVITY UNDER CONTINUOUS LIGHT

The findings in the literature regarding the effect of continuous light on dry matter production are very contradictory, mainly due to different experimental settings and other than light growth factors, as well as different plant age. Extension of daylength to 24 h gave no further increases in dry matter accumulation in cucumber, maize (*Zea mays* L.), *Chrysanthemum* (Gislerød *et al.* 1989; Warrington and Norton 1991), begonia, geranium, *Hedera*, *Kalanchoe* (Gislerød *et al.* 1989), radish (Warrington and Norton 1991; Ohyama and Kozai 1998), sunflower (Gvozdeva 1981), lettuce (Inada and Yabumoto 1989) and even decreased growth and yields of tomato and sweet pepper plants in some cases when caused such negative effects as chlorosis or blistering of leaves (Costes and Milhet 1970; Bradley and Janes 1985; Vézina *et al.* 1991). However, Murakami *et al.* (2009) reported that plants of sweet pepper grew well and bore abundant fruits under continuous fluorescent illumination, although pungency level strongly increased. Ohyama *et al.* (2005a) reported working with tomato plug transplants that did not develop leaf injuries, probably due to the alternating air temperature, that fresh weight, dry weight and leaf area of tomato plants were 41, 25 and 64% greater, respectively, under the 24-h photoperiod than under 16-h photoperiod with the same daily integrated PPF. These results suggested that using a 24-h photoperiod with relatively low PPF has the benefit of reducing both initial and operational costs for transplant production in closed systems. Under the relatively low PPF condition, the number of lamps can be decreased, resulting in the reduction in the consumption rate of electric energy of lamps, decreased requirements for cooling and the extension of lamp lifetime (Koontz and Prince 1986; Ohyama and Kozai 1998; Ohyama *et al*. 2005a). For the production of plant dry matter, often lengthening the photoperiod is more effective than increasing the illumination. Plants exposed to a low PPF for a long photoperiod generally accumulate more dry matter than plants exposed to a high PPF for a short photoperiod under the same daily integrated PPF. This phenomenon was reported in lettuce (Craker and Seibert 1982; Koontz and Prince 1986; Oda *et al*. 1989; Kitaya *et al*. 1998), radish (Craker *et al*. 1983), roses (Jiao *et al*. 1991), Benjamin Fig (*Ficus benjamina* L.) (Mortensen 1992) when plants were grown under the 24-h photoperiod vs shorter photoperiods. Craker and Seibert (1982) also observed that the lower the radiation, the greater the effect of increased photoperiod. Increased dry matter accumulation was also found in pansy (*Viola x wittrockiana* Kappert) (Langton *et al*. 2003), wine grape (*Vitis vinifera* L.) (Moshkov 1987), barley, millet, spring oilseed rape (Lisovskij and Dolgushev 1986) and beetroot (*Beta vulgaris* L.) (Lebedeva *et al*. 1978) grown under continuous light. Homma *et al*. (2009) reported that continuous irradiation by blue and especially red LED showed positive effects on growth of young tea plants (*Camellia sinensis* L.). Alfalfa seed yield was greater under continuous light compared the 18-h photoperiod (Lisovskij and Dolgushev 1986). Seeds of plants grown under continuous light had germinating capacity of 100% and were not hard, while those of plants grown under 18-h photoperiod had germinating capacity of 88% and almost all seeds were hard, i.e. required scarification.

Some tests sponsored by NASA focused on the photoperiod responses of potato cultivars, and in particular, which cultivars might be tolerant to continuous light. The rationale for this was simple: If plant growth and tuber yield could be increased with longer photoperiods, the total crop area required to sustain humans in a life support system could be reduced (Wheeler 2006). The good performance of some cultivars and the poor performance of others indicated genotypic differences in response to photoperiod (Wheeler and Tibbitts 1986a, 1986b; Yandell *et al*. 1988; Wheeler *et al*. 1991). In plants of potato cultivars that are tolerant to continuous light and did not develop leaf injuries or malformations dry matter production was greater under continuous light treatments than under the 12-h photoperiod (Wheeler and Tibbitts 1987). In contrast, the total growth of plants of intolerant cultivars was severely depressed under continuous light treatments. Initially, they grew vigorously but by 10-d-age the leaves began to show flecking and malformation. These injury symptoms intensified with age, consequently stunning total growth of these plants (Wheeler and Tibbitts 1986a, 1986b). The results of experiments suggested that all the cultivars tested were intrinsically 'short day' with regard to tuber initiation but that this tendency could be overridden with greater total light levels in some cultivars (Wheeler and Tibbitts 1986b). When plants were provided SD for the first 40 days to initiate strong tuber sinks followed by continuous light for 92 days to promote tuber bulking final tuber yields reached level, that is roughly twice that for record field yields, suggesting there is still potential for increasing yields in field settings (Wheeler 2006).

The alternation of photoperiods was found to give benefits to other crops also. Demers and Gosselin (2002) suggested that early vegetative growth and fruit production of tomato and pepper plants can be generally improved by continuous lighting for 5 to 7 weeks. However, they mentioned that such a practice should be investigated in order to determine if short-term use of continuous light might have residual negative effects on plants. A different lighting regime was proposed by Volk and Mitchell (1993) for rice (SDP), which has been selected as a CELSS candidate species for human life support in space. Greenhouse studies have shown that edible yield rates, shoot harvest index and individual panicle weight increased if the cultivar was switched from 8 h to 24 h day after panicle emergence.

Not necessarily increased vegetative yield under continuous light results in increased reproductive yield. Thus, for example, Moshkov (1987) observed that in raspberry (*Rubus idaeous* L.) fruit yield was twice lower under continuous light compared the 13-15-h photoperiods, despite the fact that vegetative mass was the greatest under continuous light. Peanut plants exposed to continuous light produced 42% more foliage biomass, but 34% less pod yield, 66% less mature seed yield, and 94% lower harvest index compared to plants grown under 12-h photoperiod (Rowell *et al*. 1999).

There are findings that exposure to continuous light at high latitudes stimulates dry matter production. When plants are transferred beyond the Arctic Circle some species develop giantism (Shavrov 1961). Thus, onions *Allium altaicum* Pall. and *A. atrosanguineum* Schrenk from the Khibini Mountains were twice as large as plants from the natural habitats in the Altais and Alma-Ata (Kazakhstan) and the size and number of their generative organs were 15,5-2 times greater compared to natural ones (Shavrov 1961). In the 'Holt' cultivar of Kentucky bluegrass (*Poa pratensis* L.) at high latitudes large effects on plant dry weight and leaf area were related to significant influence of continuous light upon leaf anatomy (Hay and Heide 1983). From leaf impressions, it was established that the epidermal cells of leaf blades were longer and broader in LD (continuous light) than in SD controls. It was concluded that continuous light stimulated both cell extension and division. Furthermore, it was shown, using leaf sections, that the higher leaf area ratios under continuous light were not due solely to increased succulence, but also to modest decreases in leaf thickness and number of cell layers (Hay and Heide 1983). There were also indicated some changes in the Arctic in the anatomy of organs in a number of introduced plant species. For example, crested gentian plants (*Gentiana septemfida* Pall.) were characterized by expanded mesophyll cells of leaves and reproductive organs and prolonged meristematic activity of cells located near conducting bundles. Owing to these changes, introduced plants had the ability of long and intensive growth (Shavrov 1961).

There is no universal agreement among authors who have reported a dry weight gain as to the mechanisms involved in the plant response to continuous light. Some authors relate stimulation of biological productivity of plants under continuous light to increased tillering and lateral branching. For example, stimulated tillering was observed in temperate grasses under continuous light (Simonsen 1985). However, Solhaug (1991) observed the opposite effect when SD (8 vs 24 h) increased tillering in 5 grass species. Increased branching was observed in many plants transferred from different geographical regions of the world to Kola Peninsula in the Russian Arctic (Shavrov 1961), where the period when the Sun is continuously in the sky lasts up to 53 days. Even larger (up to 100 days) is the period of so-called 'white nights' and the period with nights without complete dark is up to 160 days. Besides, according to Langton *et al.* (2003) in some plant species increases in plant biomass production due to prolonged photoperiod result from actions related to increases in leaf area and chlorophyll (chl) content per unit of leaf area. However, increases in plant dry weight are unlikely to mirror precisely the observed increases in leaf greenness. For example, in kale (*Brassica oleracea* L. var. *acephala* D.C.) an increase in photoperiod resulted in increased pigment accumulation, but maximum concentrations of pigments were not required for maximum biomass production (Lefsrud *et al*. 2006). Plants from two groups of potato cultivars grown under continuous irradiation, which differed 10-fold in plant dry matter production did not differ significantly in leaf chl concentration (Cao and Tibbitts 1991). According to Solhaug (1991) an increase in plant leaf area is much more important than an increase in the chl content per unit leaf area for increasing light absorptance. Under conditions of Kola Peninsula (beyond the Arctic Circle) the most active chloroplasts in potato plants are those that are large, with loose structure and small osmiophilic granules. Plants with such chloroplasts have large leaf area and high dry matter production under conditions of long polar day and short growing season (Shahov 1965). It was shown by Miroslavov *et al.* (1998) that Arctic plants are often characterized by chloroplasts with deep invaginations or excrescences, more compact intracellular arrangement of plastids, larger number of mitochondria, more branched endoplasmic reticulum and numerous lipid vesicles.

The modifying influence of different growth factors, such as temperature, light intensity, $CO_2$ enrichment, water and fertilizer supply etc. under continuous lighting regime has been reported by many authors. It was shown for six grass species that LD without increase in daily photosynthetically active radiation (PAR) stimulated dry matter (DM) production most at low temperatures (Solhaug 1991). It was known that temperate grasses increase DM production in LD via increased leaf area ratio (LAR) which more than compensates for reduced net assimilation rate (NAR) in LD (Hay and Heide 1983; Solhaug 1991). Solhaug (1991) suggested the following mechanism of LD stimulation of DM production. Higher LAR in LD than in SD was mainly a result of the increased specific leaf area (SLA, leaf area per unit leaf dry weight) in LD, since leaf weight ratio (LWR, the proportion of DM allocated to the leaves) was almost unaffected by daylength. When SD-propagated plants are placed in LD, a rapid increase in SLA occurs. In addition, more assimilates are allocated to growth, which together with increasing SLA lead to increased leaf area in LD. Since the NAR is only slightly reduced, photosynthetic capacity per plant will increase. This creates a positive feedback system, since more assimilates will be available to leaf growth due to higher photosynthesis per plant.

Results of Masuda *et al.* (2006) indicated that the enhancement of dry mass production in pepper plants by overnight supplemental lighting is more profound when the daytime solar radiation is low. Kitaya *et al.* (1998) showed that at the same PPF, DM of lettuce plants was increased by 25% to 100% with 24-h photoperiod compared to 16-h. However, at the same daily light integral (DLI), the longer photoperiod (24 h vs 16 h) promoted growth of lettuce plug transplants under the low $CO_2$ concentration, but not under the high $CO_2$ concentration.

Manipulation by plant mineral nutrition was shown to be the possible way to increase yield under conditions of continuous lighting. Some cultivars of hard wheat did not yield a harvest under continuous light when provided by standard mineral nutrition. However, development of nutrient medium with increased concentrations of all nutrients and mixed nitrate and ammonia nitrogen allowed successful cultivation of wheat under continuous light (Lisovskij and Dolgushev 1986). The use of vermiculite substrate in combination with plant mineral nutrition varied during plant ontogeny stimulated significantly greenhouse production of some ornamental plants (calla lily (*Zantedeschia aethiopica* (L.) Spreng.), Barberton daisy (*Gerbera jamesonii* Bolus ex Hook.f.), Jersey lily (*Alstroemeria* spp.), amaryllis (*Hippeastrum* spp.), cucumber and tomato plants under conditions of polar day on Kola Peninsula (Russian Arctic) (Ivanova *et al.* 2006).

## ASSIMILATE PARTITIONING UNDER CONTINUOUS LIGHT

Continuous light affects not only DM production but also the partitioning of DM within the plant. Thus, in six temperate grass species grown under continuous light more DM was allocated to leaf sheaths and stems than in SD, while more DM was allocated to the roots in SD. The greatest effect was found in smooth brome (*Bromus inermis* Leyss.) in which 24-h photoperiod more than doubled the proportion of DM in the leaf sheaths and stems, while reducing the proportion of DM in the roots by nearly 50% (Solhaug 1991). However, these findings do not support those of Hay and Heide (1983) who found that continuous light had very little influence upon the distribution of dry matter between culms, leaves and stolons in Kentucky bluegrass. Continuous light did not change partitioning of DM in wheat, barley, cucumber and soybean at early stages of development compared to other photoperiods (Markovskaja and Sysoeva 2004). In black currant (*Ribes nigrum* L.) continuous light favored accumulation of dry matter in leaves and stems, while 14-h photoperiod was preferred to root growth (Lisovskij and Dolgushev 1986).

In some experiments continuous light enhanced vegetative growth at the expense of reproductive growth. Thus, in peanut plants continuous light reduced pod and seed yield by delaying or decreasing assimilate partitioning to reproductive organs, which resulted in 94% lower harvest index compared to that of plants under 12-h photoperiod (Rowell *et al.* 1999). Similarly, vegetative mass of raspberry bushes was the greatest under continuous light, but fruit yield was twice lower compared the 13-15-h photoperiods (Moshkov 1987). In a greenhouse study aimed at increasing biomass partitioning to rice grain, plants were switched to continuous light after different periods of time under 8-h photoperiods. There was a positive correlation between the length of continuous light treatments and non-grain biomass, but grain yield did not increase in continuous light (Volk and Mitchell 1993).

The role of storage organs in the biomass partitioning within plants under continuous light remains unclear. For the understanding of source-sink interactions under continuous light the effect of increased source activity (i.e. photosynthesis – generated by a 24-h photoperiod) on two species of onion that differ in their sink capacity (bulbing vs. non-bulbing) was studied (Gestel *et al.* 2005). Plants showed a different response to photoperiod in biomass partitioning, such that over half of the biomass in both *Allium* species in the 12-h photoperiod was present as leaves, while in the 24-h photoperiod up to 84% of total mass was present as bulbs. This is in accordance with research by Garner and Allard (1923) and Kato (1965), who reported that in onions SD promoted leaf growth, while LD stimulated bulb production, even when sucrose was injected into onion leaves. This suggests that carbohydrate accumulation promotes bulb development only when photoperiod exceeds a specific duration. Long photoperiods and high irradiances were also shown to increase the percentage of plant assimilates transferred to the radish storage organs. For radishes exposed to an irradiance of 113 W $m^{-2}$ and a photoperiod of 24 h, almost 90% of the plant was storage organ (Craker *et al.* 1983). The production of early-season radish varieties decreased when the day length was extended from 12 to 24 h. They formed flower stalks, but did not form storage organs. On the contrary, full-season varieties had much higher production under continuous light by forming storage organs quicker (Lisovskij and Dolgushev 1986). In the experiments by Tihomirov *et al.* (1976) radish plants grown under continuous light provided by xenon lamps with PAR of 400-650 W $m^{-2}$ had very high production of storage organs, but the yield per unit of light energy was decreased considerably compared to other photoperiods. In experiments with turnip (*Brassica rapa* L. var. *rapa* (L.) Hartm.) (Akira *et al.* 1988) the greater plant biomass and storage root weight were obtained under 24-h photoperiod. Plant growth and accumulation of assimilates in storage roots were stimulated by higher irradiance and elevated $CO_2$ concentration under continuous light.

Quite the opposite assimilate distribution pattern was observed in plants under natural conditions of Kola Peninsula (Russian Arctic). Long photoperiods decreased the percentage of plant assimilates transferred to the sugar-beet storage organs, so that weight of leaves was twice as much as storage organ weight (Stanko 1965). Zhurbickij and Vartapetjan (1956) and Kisljakova (1965) have shown that long polar day and low irradiance are two main unfavourable factors for starch accumulation in potato tubers. However, these findings are in contrast with results obtained by Kardo-Sysoeva (1963) who came to a conclusion that the main cause of low starch content in potato tubers in Yamalo-Nenetsky region (western Siberia, Russia, the latitude of the Arctic Circle) is low soil temperature. Despite the fact that in experiments temperature increase affected positively starch synthesis is potato tubers under conditions of Kola Peninsula, all obtained experimental data gave grounds to Kisljakova (1965) to make conclusion on the leading role of light factor in starch accumulation.

Findings from controlled environment studies at NASA showed that despite the ability of some potato cultivars to grow and tuberize under continuous light, SD tendencies were still apparent. For example, harvest index, which is an indicator of the partitioning to tubers, was nearly always greatest under SD, and hence efficiencies for converting light into edible biomass were greatest under SD (Wheeler and Tibbitts 1986a; Wheeler *et al.* 1991). These observations suggested that yields might be optimized if strong induction could be combined with high total light. This idea was tested by moving plants between a 12 h light/12 h dark and a 24-h light environment at different stages of growth (Wheeler 2006). The results showed that at equal total irradiance, plants given SD early in growth followed by continuous light later in growth produced greater tuber yields than plants given continuous light followed by SD (Wheeler and Tibbitts 1997). This suggests that it is best to first establish strong tuber initiation and then follow with high total light to sustain bulking (Wheeler and Tibbitts 1997). In contrast to results obtained by Kisljakova (1965) in research by Wheeler *et al.* (1986) harvest index of potato plants decreased with increasing temperatures under continuous light. Their results showed that cooler temperatures could be used to offset the less inductive influence of a long photoperiod, i.e. under cooler temperatures the potato becomes less obligate for dark period stimulation of tuberization. Thus, the influence of continuous light or supplementary lighting seems important not only to enhance growth, but also to influence dry matter distribution to the fruits, flowers and storage organs, in order to produce a high yield.

## PHOTOSYNTHESIS UNDER CONTINUOUS LIGHT

Findings in the literature on the long-term impact of continuous light on photosynthesis are quite contradictory. There are data testifying to the decrease of photosynthesis under continuous light. For example, Stutte *et al.* (1996) have shown that in potato plants grown under 24-h photoperiod, photosynthesis was 33% lower than in plants grown under 12-h photoperiod. The reduction in photosynthesis was attributed to high starch accumulation in leaves, suggesting that photosynthate production (i.e. source activity) was greater than photosynthate utilization (i.e. sink activity). Therefore, higher source activity relative than sink activity may have initiated the downregulation of photosynthesis at the protein or transcriptional level, thereby lowering the amount and/or activity of Rubisco. However, quite the opposite, Cao and Tibbitts (1991) showed that the lower net photosynthesis in potato plants grown under continuous light was not associated with an excess carbohydrate accumulation in the leaves. Moreover, cultivars differed in their physiological response to continuous irradiation and some cultivars did not demonstrate decreased $CO_2$ assimilation. The inhibition of net $CO_2$ assimilation in stunted plants was not also due to a limiting amount of chl or to $CO_2$ in the leaf tissues. Wheeler and Tibbitts (1986a) suggest that intolerant to continuous light potato varieties are incapable of sustaining continuous photosynthetic activity, while the tolerant varieties are capable of sustaining the activity. In tests with potato, in which the photoperiod was changed from 12 h to 24 h, photosynthetic rate dropped immediately following the change to continuous light as a result of some 'scorching' of the upper canopy leaves (Wheeler 2006). It is of interest to note the slight negative effect of elevated $CO_2$ on net photosynthesis rates observed in some potato cultivars (Wheeler and Tibbitts 1989; Cao *et al.* 1994). Total plant biomass and tuber yields showed similar trends, where elevated $CO_2$ and increased PAR increased yields under a 12-h photoperiod, but had only a slight or even negative effect under continuous light (Wheeler *et al.* 1991). Wheeler and Tibbitts (1989) offered as possible explanation for this that the use of continuous lighting at 450 $\mu$mol $s^{-1}$ $m^{-2}$ may already be 'pushing' the potato plants to their maximum growth potential. Models of tuber yield developed by Yandell *et al.* (1988) predicted little advantage from $CO_2$ enrichment under continuous light when irradiance levels exceed 500 $\mu$mol $s^{-1}$ $m^{-2}$ PPF. It is possible that assimilation rates in potato leaves were suppressed by some photosynthetic feedback inhibition under continuous lighting and high $CO_2$ (Wheeler and Tibbitts 1989).

The use of continuous light caused a reduction of the photosysnthesis rate in photoperiod-sensitive tomato, but did not affect photosynthesis rates in less-photoperiod-sensitive sweet pepper (Demers 1998). Demers and Gosselin (2002) suggest that the increased accumulation of starch generates, by a feedback effect, an overload of the Calvin cycle, which gradually causes the decrease of the $CO_2$ fixation rate. Demers *et al.* (1995) have reported that pepper plants were less-efficient than tomato plants in using light for $CO_2$ fixation, but were more efficient in dissipating the extra energy received. This may explain why pepper plants are less sensitive to continuous light than tomato plants, although both species are of the *Solanaceae* family and require similar conditions.

Gestel *et al.* (2005) in order to test whether photosynthesis downregulation occurs due to carbohydrate feedback used onions that differed in bulb-forming capacity. In *Allium fistulosum*, a non-bulbing onion, photosynthetic downregulation was observed under continuous light as indicated by reductions in the light- and $CO_2$-saturated photosynthetic capacity, reduced maximum rate of carboxylation by Rubisco, reduced maximum rate of electron transport and 3-fold higher foliar sugar concentration. In contrast, the photosynthetic and biochemical capacity of *Allium cepa*, a bulb-forming onion, was not affected by exposure to 24-h photoperiod, presumably because substantial amounts of foliar carbohydrates were re-allocated to bulbs. Thus, carbohydrate concentration may not fully be responsible for regulating photosynthesis.

Foliar nitrogen may also be a key regulator of photosynthesis. In experiments by Gestel *et al.* (2005) in both *Allium* species, 24-h plants had much lower N levels compared with 12-h plants. Usung N as a quantitative measure of Rubisco content suggests that Rubisco levels for borth *Allium* species in 24-h plants are much lower than in 12-h plants. However, Rubisko activity was only reduced in *A. fistulosum* and not in *A. cepa*. Therefore, reduced Rubisco activity, potentially initiated by higher foliar carbohydrate concentration in *A. fistulosum,* could have been primarily responsible for the observed photosynthetic downregulation (Gestel *et al.* 2005). This is consistent with Paul and Foyer (2001) who stated that when carbohydrate levels reached a threshold, downregulation of photosynthesis was initiated to rebalance the source-sink ratio. The formation of a storage organ enabled *A. cepa* to balance its source-sink ratio to a greater degree than *A. fistulosum*, thereby maintaining Rubisco activity at similar levels to *A. cepa* in the 12-h photoperiod (Gestel *et al.* 2005).

Lower net photosynthetic rate of peanut (*Arachis hypogaea* L.) plants grown under 24-h photoperiod compared to 12-h photoperiod coupled with the lower stomatal conductance (Rowell *et al.* 1999) suggesting that plant may have been sufficiently stressed to cause a partial closure of the stomates, thereby influencing the gas exchange rates of these plants. However, carbon fixation efficiency was significantly lower among plants grown under 12-h light period. The decrease reflected a probable diversion of the Rubisco enzyme from oxygenation to carboxylation in plants grown under continuous light.

Research conducted in the Arctic under natural conditions of continuous light have shown that plants there utilize solar energy of a wider spectrum range (Shahov 1965) and the findings regarding photosynthetic activity of plants are quite contradictory to those obtained in greenhouse research. Thus, there are reports that under conditions of Kola Peninsula photosynthesis may measure up to very high values, up to 40-80 mg $CO_2^{14}$ per $dm^2$ h in barley, wheat, radish and some wild plants. Net photosynthesis of 7-8 g DM per $m^2$ day was reported for potato (Shahov 1965). Under natural conditions at high latitudes photosynthesis may occur at lower light intensities providing greater DM accumulation per day due to longer photoperiod (Shul'gin 1973). Continuous light ensures positive leaf net $CO_2$ flux over the entire 24-h photoperiod in plants both under natural conditions (Shvecova and Voznesenskij 1970; Luk'janova *et al.* 1986) and in greenhouses (Afanasjeva 1970). The lack of diurnal rhythm in photosynthesis under continuous light was reported for Benjamin Fig, although it was found under 18-h photoperiod, indicating that the plant benefits from continuous light. Indeed, dry weight increased progressively with increasing lighting periods between 16, 20 and 24 h $day^{-1}$ in this species (Mortensen 1992). More studies focused on how the photoperiod affects the carbon metabolism of plants, which could be linked to development of negative effects on plants grown under continuous light are needed in order to confirm the hypotheses advanced.

## LEAF PIGMENT CONTENT UNDER CONTINUOUS LIGHT

The effect of photoperiod on leaf pigment content is varied. For example, Fukuda *et al.* (2000) found that additions of night supplemental lighting increased chl concentrations in lettuce, pakchoi (*Brassica rapa* L. subsp. *chinensis* P. Hanelt) and tsukena (*Brassica rapa* L., subsp. *campestris* A.R. Clapham), but this was not found to be the case by Solhaug (1991) who reported that plants of four temperate grass cultivars cultivated in SD (8 h) contained about 50% more chl per unit leaf area or fresh weight than plants cultivated under 24-h photoperiod. However, Solhaug (1991) came to the conclusion that the reduction of chl content per unit leaf area in plants cultivated under continuous light *per se* seems not to be the mechanism causing reduced photosynthetic rate of high-latitude grasses in LD. Increasing the day-extension lighting from 16 h to 24 h gave no further intensification of greenness in four bedding plant species: geranium, impatiens (*Impatiens walleriana* Hooker), pansy and petunia (*Petunia x hybrida* (Hooker) Vilmorin) (Langton *et al.* 2003). In tomato and pepper plants, foliar chl content was negatively correlared to lengthening of the photoperiod (Dorais 1992). Lower foliar chl as determined on a dry weight basis, was measured in tomato plants cultivated under a 24-h photoperiod (Bradley and Janes 1985). However, when the chl content of leaves was calculated on a leaf area basis, no significant difference was found between photoperiods of 12 h and 24 h. Despite the development of visible mottled chlorosis soon after exposure of tomato plants to continuous light, pigment levels were not measurably lower than those of controls grown under a 12-h photoperiod until injury was quite severe, indicating that pigment levels in green areas of the leaf compensated for pigment losses in chlorotic areas (Globig *et al.* 1997). With respect to electron transport capacity through photosystems, activities per unit of chl in photosystem II (PSII) and photosystem I (PSI) of tomato plants and PSI of pepper were not affected by photoperiodic treatments, while PSII activity in pepper increased under continuous lighting (Dorais 1992). Photosystem activity in tomato plants correlated positively to chl content of leaves, while this relationship was not found in pepper plants. This explains why, unlike pepper plants, PSII and PSI activities of tomato plants correlated negatively with extension of the photoperiod. Under continuous light, a decrease in the photosynthetic rate was measured in tomato plants, while it increased in pepper plants. No significant correlation was found in either species between photosynthetic rate and leaf chl content or photosystem activity. Both tomato and pepper plants adapt to continuous light by modifying the distribution of chl among the photosystems and altering the size of photosystems. In tomato plants, these photo-adaptation phenomena are actually an increase in the proportion of chl associated with PSII compared with PSI and a decrease in the size of PSI following reduction in the size of its antenna (LHCPI). In pepper plants, a reduction in the size of PSII was compensated by an increased activity (Dorais 1992). Dorais (1992) concluded that reduced efficiency of tomato plants in benefiting from long photoperiods is not due to a lower capacity of electron transport through the photosystems caused by photoinhibition, but rather to restrictions in the carbon metabolism, which in turn leads to partial photooxidation of the chl and is perhaps responsible for development of foliar chlorosis.

The research into the effect of continuous light on carotenoid accumulation is limited in higher plants. Lefsrud *et al.* (2006) reported maximum accumulation of lutein and β-carotene occured in kale under the 24-h photoperiod. Continuous light caused reductions in carotene and xanthophylls content in tomato and sweet pepper plants (Demers 1998). Leaf chlorosis and loss of pigments were more important and occurred earlier in tomato plants than in sweet pepper. Compared to sweet pepper plants, EPS ration (epoxidation state of the pigments of the xanthophylls cycle) was lower in tomato, indicating a greater need for energy dissipation and a more important state of stress caused by excessive light. Pigments such as carotene and xanthophylls play a significant role in the protection of the photosynthetic apparatus against damage that could be caused by an excess of light. Carotene and xanthophylls levels were higher in sweet pepper plants than in tomato. Thus, sweet pepper has a better protection against the degradation of chl, which would explain why leaf chlorosis appeared later and were less severe in sweet pepper (Demers and Gosselin 2002).

## PHYSIOLOGICAL DISORDERS UNDER CONTINUOUS LIGHT

Daily timing of supplementary lighting can be manipulated to maximize crop response and therefore it is widely used in greenhouse production (Costes and Milhet 1970; Koontz and Prince 1986; Logendra *et al.* 1990; Moe 1997). Under extended photoperiods, however, many sensitive species tend to develop important physiological disorders. The decreased ability to utilize supplemental lighting is associated, notably, with the appearance of intervascular chlorosis. Light injury symptoms caused by exposing plants to continuous light were reported for several species including tomato (Hillman 1956; Bradley and Janes 1985; Vézina *et al.* 1991; Warrington and Norton 1991; Cushman *et al.* 1995; Murage *et al.* 1996), coleus (*Solenostemon scutellarioides* (L.) Codd), chrysanthemum (Warrington and Norton 1991), eggplant (Murage *et al.* 1996), potato (Wheeler and Tibbitts 1986a; Tibbitts *et al.* 1990; Cao and Tibbitts 1992; Stutte *et al.* 1996), radish (Craker *et al.* 1983; Warrington and Norton 1991), cowpea (*Vigna unguiculata* (L.) Walp.) (Ohler and Mitchell 1996), onion (Gestel *et al.* 2005), cucumber (Wolff and Langerud 2006), geranium, cotton, buckwheat (*Fagopyrum esculentum* Moench.) (Arthur and Harvill 1937). In contrast, some other plants do not appear to suffer from leaf injury under continuous light. This was reported for lettuce (Craker *et al.* 1983; Kitaya *et al.* 1998), sweet pepper (Murage and Masuda 1997), rise (Volk and Mitchell 1993), peanut (Rowell *et al.* 1999), Kentucky bluegrass (Hay 1990), meadow foxtail (*Alopecurus pratensis* L.), Hungarian brome (*Bromus inermis* Leyss.), cocksfoot grass (*Dactylis glomerata* L.), meadow fescue (*Festuca pratensis* Huds.), timothy (*Phleum pretense* L.) (Solhaug 1991), soybean (Davydenko *et al.* 2004), wheat, barley, millet, pea, alfalfa, sunflower (Lisovskij and Dolgishev 1986), kale (Lefsrud *et al.* 2006), turnip (Akira *et al.* 1988), roses (Jiao *et al.* 1991). Different potato cultivars have been found to vary widely in their response to continuous irradiance. Some of cultivars grew well and had better production under continuous irradiation, whereas other cultivars showed adverse growth responses developing brown and black flecking on the plant leaves initially and chlorosis and necrotic lesions as the plants aged (Wheeler and Tibbitts 1986a; Tibbitts *et al*. 1994). Wheeler (2006) noted that not surprisingly cultivars selected for high latitudes were more tolerant to long photoperiods. Similarly, cultivars of loose-leaf lettuce differed in respect of developing physiological disorders under continuous light (Koonts and Prince 1986).

In addition to duration of lighting per day, other aspects of light energy, such as light quality and quantity also play roles in the development of the effects of continuous light. Thus, the severety of leaf chlorosis in tomato and pepper plants caused by continuous light varied with the type of lamps (high pressure sodium versus metal halide) used to provide supplemental light and was modified by the presence or absence of natural light (Demers 1998; Demers and Gosselin 2002). The addition of far-red light as supplement to the white light greatly reduced light injury symptoms on tomato leaves caused by the white light (Globig *et al*. 1997). Differences in the severity of the foliar chlorosis were observed depending on the type of lamps used to grow eggplants (Murage *et al*. 1997), geranium, cotton, buckwheat (Arthur and Harvill 1937) under continuous light. The extent of the leaf injury under continuous illumination was strongly influenced by the daily quantity of light received by the plants. It was shown for eggplant (Murage *et al*. 1997), lettuce seedlings (Oda *et al*. 1989) and Arabidopsis (Massa *et al*. 2007) that the degree of leaf injury was positively correlated to the increase in the photosynthetic photon flux density (PPFD) under continuous illumination. However, Murage *et al*. (1997) clearly indicated the predominant effect of the photoperiod over light quantity on the induction of the leaf injury.

Even though it has been known for a long time that exposing some plants to 24-h photoperiod causes the development of leaf chlorosis and growth reductions, the cause of these problems remains unclear. A short review on the factors possibly involved in the development of the negative effects of long photoperiods on tomato and sweet pepper plants was published by Demers and Gosselin (1999). It was suggested (Bradley and Janes 1985; Logendra *et al*. 1990; Dorais 1992) that the starch and soluble sugar accumulations in leaves of tomato plants could be related to the development of the leaf chlorosis under continuous light. Studies on some other species support the hypothesis of a relationship between leaf chlorosis development and starch accumulations. For example, continuous light caused increased leaf starch and hexose accumulations and leaf chlorosis of eggplants (Murage *et al*. 1996). However, eggplants growing under continuous light but in a $CO_2$-free atmosphere for 12 h per day accumulated less starch and hexoses, and did not develop leaf chlorosis. There are indications that accumulations of starch and soluble sugars are not caused by a limiting sink capacity. Demers *et al*. (1998a) concluded that if leaf photosynthate accumulation is related to leaf chlorosis and decreased growth and yields, it is possibly the inability of the leaf to export photosynthates out of the leaf that is the liming factor.

In tomato, the use of continuous light caused, in addition to the foliar chlorosis and increased foliar contents in starch and hexoses, a reduction of the photosynthesis rate and of the activity of the sucrose phosphate synthase (SPS) enzyme (Demers 1998). The reduction of SPS activity occurred in 2-4 weeks after the increase in starch and hexoses. It is, thus, impossible that the reduction of the SPS activity is responsible for these accumulations. However, Demers and Gosselin (2002) suggest that it is possible that the SPS activity *in vivo* is limiting, which would explain the hexose increase. This suggests the limiting step of the export of photosynthases in the synthesis of sucrose and would explain the absence of growth and the productivity increase under continuous light. Furthermore, the increased hexose levels in the cytoplasm, by a feedback effect, would limit the export of the triosephosphate (photosynthesis products) out of the chloroplast, which would then be redirected towards starch synthesis, thus explaining the increased starch contents. Moreover, the increased accumulation of starch would generate, by a feedback effect, an overload of the Calvin cycle, which would gradually cause the observed decrease of the $CO_2$ fixation rate. Are the starch accumulations responsible for the leaf chlorosis in tomato? It is possible that the overload imposed on the Calvin cycle (decreased photosynthesis) could limit the use of the reducing potential (ATP, NADPH) produced by the luminous phase of photosynthesis, thus causing an overload on the electron transport chain and the photo-oxidation of the chl (decrease in the leaf chl contents), and thus explaining the observed leaf foliar chlorosis. Transgenic tomato plants (overexpressing SPS) that have higher photosynthesis rates and accumulate less starch and more sucrose than non-transformed plants (Galtier *et al*. 1993, 1995; Micallef *et al*. 1995) could be used in future studies to test if accumulations of starch in leaves are responsible for the development of chlorosis observed in plants exposed to continuous light (Demers and Gosselin 2002). In sweet pepper, the use of continuous light caused an increase in the leaf starch and sucrose contents, but did not affect leaf hexose contents, photosynthesis rates and SPS activity (Demers 1998). The increased foliar contents in sucrose indicate that SPS activity in sweet pepper is not limiting as in tomato. Increased accumulation of starch in sweet pepper plants exposed to continuous light would be explained by the fact that continuous light results in a longer period of time over which starch synthesis occur, but without overloading the starch synthesis pathway. Thus, starch accumulation in sweet pepper under continuous light would not be important enough to cause a reduction in $CO_2$ fixation (no overload of the Calvin cycle). Increased leaf contents in sucrose suggest that sucrose export would be possibly limiting. This would explain why the growth and the productivity of the sweet pepper plants do not increase under continuous light. Moreover, compared to tomato, higher levels of carotene and xanthophylls in pepper leaves probably provided a better protection of the photosynthetic apparatus against excessive light, plus preventing the destruction of chl and development of leaf chlorosis in pepper (Demers and Gosselin 2002).

The results for leaf starch content in cucumber exposed to continuous light in the study by Wolff and Langerud (2006) gave no support to the hypothesis that it is hyper-accumulation of starch that causes leaf injuries and lower plant production under continuous light. However, they admitted that leaf sampling and analysis were performed at a rather late stage in injury development and nothing was known about the starch status previous to visible symptoms. In two groups of potato cultivars (those that are stunted and injured by constant light and those that grow well) the lower net $CO_2$ assimilation rates in stunted plants were not associated also with an excess carbohydrate accumulation in the leaves (Cao and Tibbitts 1991).

Dorais *et al*. (1995) reported that under continuous light, the situations might happen when photosynthesis efficiency is reduced while interception of the incoming light continues unabated. It is therefore, possible that a direct leakage of electrons to molecular oxygen occurs, enhancing the generation of toxic oxygen species. This can damage the ultrastructure and function of chloroplasts, and photosynthetic pigments leading to leaf chlorosis (Foyer *et al*. 1994). Thus, it was hypothesized that the leaf injury observed under continuous light in sensitive species is attributed to photooxidative stress. From the results of Murage and Masuda (1997), it emerged quite clearly that continuous light triggers photooxidative damage in eggplant as evidenced by the incidence of chlorosis, decreased chl and the synchronized increases of superoxide dismutase (SOD), peroxidase (POD) and catalase (CAT) activities. On the other hand, pepper plants did not appear to suffer from photooxidative damage and thus grew normally under continuous illumination. Continuous light did not enhance the activities of SOD and POD in leaves of pepper, but the CAT activity was significantly higher in pepper than in eggplants. These results are supported by Masuda *et al.* (2002) who also suggested that the superoxide radical is associated with light-induced leaf injury in eggplants. However, there are reports in the literature that argue that the light leaf injury observed under continuous light is correlated to photooxidative damage. Thus, Gestel at al. (2005) reported that leaf necrosis and chlorosis exhibited in both bulbing and non-bulbing onion species in the 24-h photoperiod was not due to photodamage, because photosynthetic light compensation point was higher in both species exposed to continuous light, which suggests that plants grown in 24-h photoperiod were less efficient using absorbed light at low irradiance and had acclimated to a high light environment. The excess light energy would then be expected to be utilized in generating oxygen radicals, leading to the subsequent photooxidation of plant pigments (Foyer *et al.* 1994).

Interesting results obtained Cushman and Tibbitts (1996) that potato cultivar 'Kennebec', which severely injured by constant light when propagated from tissue-cultured plantlets, also was injured when plants were propagated from small tubers pieces (approximately 1 g). However, plants did not develop injury when propagated from large tuber pieces (approximately 100 g). Authors suggested that plant vigor and carbohydrate translocation play role in controlling injury development. Cushman and Tibbitts (1998) also noted that in many ways the injury of plants grown under continuous irradiation and constant temperature resembles the effects of ethylene exposure: leaf abscission, chlorosis, reduced leaf area, and increased leaf thickness. Studies on potato and tomato (Cushman and Tibbitts 1998; Jensen and Veierskov 1998; Wheeler *et al.* 2004) support the hypothesis that ethylene metabolism is one of the possible mechanisms by which plants are injured by continuous irradiation, but the casual chains are so far not elucidated.

It was shown on tomato plants that that growth and yields reductions as well as leaf chloroses observed under continuous light have not been related to mineral nutrition problems (Withrow and Withrow 1949; Demers *et al.* 1998a). However, there are reports on some success in improving appearance of plants grown under 24-h photoperiod by increasing fertilization. Thus, increased liquid fertilization reduced the purpling of leaves of Arabidopsis plants grown under continuous light (Massa *et al.* 2007). Leaf necrosis that developed at the high PPFD in lettuce leaves was partly alleviated by adding more nitrogen to the nutrient solution (Koontz and Prince 1986). High concentration of calcium reduced leaf chlorosis and increased fruit yield in mini-cucumber production under supplemental lighting (Hao *et al.* 2009). In the same study, adding blue light alleviated leaf chlorosis symptom but did not further improve mini-cucumbers fruit yield compared to high pressure sodium lihjting along (Hao *et al.* 2009).

It was reported long ago that light injury was reduced at low temperatures (Roodenburg 1940; Withrow and Withrow 1949). Daily temperature alternations has been shown to be effective in preventing physiological disorders in plants and inhibition of growth caused by continuous daily light periods (Hillman 1956; Went 1957; Kristofferson 1963; Tibbitts *et al.* 1990; Omura *et al.* 2001). As early as in the 1930s Bünning (1931) showed that, under continuous light, scarlet runner (*Phaseolus multiflorus* L.) plants subjected to variable temperature regime had much less severe leaf chlorosis compared to those subjected to a constant temperature regime. Later Hillman (1956) and Kristofferson (1963) observed that not all variable temperature regimes are equally effective in preventing physiological disorders in tomato plants caused by continuous light, but day/night differential should be of 8-10°C or greater. It was suggested that for a plant previously exposed to high temperature, a low temperature light period is equivalent to a dark period as far as photoperiodically-sensitive system is concerned. But, since several experiments showed that this apparent equivalence of low temperature light with darkness no longer holds in an injurious alternating light-dark schedule, this simple hypothesis was abandoned, and temperature change regarded as the significant factor in preventing injury. Recently the interest of researches to the potential use of a 24-h photoperiod with alternating air temperatures for plant production in closed systems has increased. Ohyama *et al.* (2005b) have shown that physiological disorders (chlorosis and/or necrosis) were not observed under the 24-h photoperiod in tomato plants grown at alternating air temperatures of 28/16°C. In our studies we observed that daily short-term exposures of cucumber plants to low temperature (12°C) decreased the severity of chlorosis caused by continuous light (unpublished data). The results obtained from the study by Tibbitts *et al.* (1990) on potato cultivars show that temperature fluctuations under constant irradiation have promotive effect, not only on shoot growth and dry matter accumulation, but also on tuberization in some potato cultivars indicating that the injury to potato plants grown under constant irradiation and temperature is not simply a light response, as shown by the lack of injury under fluctuating temperatures. It supports the conclusion made by Wheeler and Tibbitts (1986b) that potato plants injury by constant light is not photoperiodic in nature, as shown by the lack of injury under the dim daylength extension treatments. This is consistent with the effective growth of potatoes in the field plantings in northern latitudes under LD, for these areas always have some diurnal temperature fluctuation during the growth period (Garner and Allard 1923; Pohjakallio 1953).

Murage *et al.* (1997) showed that the temperature cycle under continuous illumination had a big influence on the leaf carbon metabolism in eggplant. In a non-injurious temperature cycle of 28/15°C, the accumulation of starch, sucrose, glucose and fructose was significantly reduced compared with the injurious temperature regimes of 25/25 and 25/20°C. This suggested that the $CO_2$ assimilation must have been drastically checked during the period of low temperature. At the same time, it is also possible that the metabolism of starch and sugars into other metabolites and their subsequent translocation from the leaves might have been enhanced greatly at 28/15°C.

It is clearly shown that the leaf injury under continuous irradiation is not simply a light response alone, but a result of a strong interaction between the light period, quality and quantity on the one hand, and on the other, the thermoperiod and that they exert their effects on the photosynthetic activity and subsequently the carbon metabolism (Murage *et al.* 1997). However, it is still not clear whether the adverse effects of these factors during induction and expression of the leaf injury are a manifestation of the buildup of carbohydrates, particularly starch, in the chloroplasts leading to the systematic destruction of chl as proposed by Bradley and Janes (1985) or a culmination of the activities of other processes such as photooxidative damage to the leaf pigments (Wise and Naylor 1987). Thus, further investigations are required in order to elucidate the causative mechanism.

Pettersen *et al.* (2006) found that a variation in the air humidity can counteract the negative effect of continuous lighting on the keeping quality of roses. The reduction in the keeping quality of roses caused by continuous lighting is related to malfunctioning stomata and excessive water loss in indoor conditions (Mortensen and Fjeld 1998; Mortensen and Gislerød 1999). However, it was found that a daily 6-h period with low air humidity was sufficient to enhance considerably the vase life of roses under continuous lighting as compared to constant high air humidity (Pettersen *et al.* 2006). The result was explained by the fact that leaves developing at high relative air humidity (RH) failed to respond to post-production conditions as leaves were unable to close their stomata and therefore control water loss. However, plants grown under conditions inducing daily stomatal closure, caused by a period of low RH, were able to close their stomata, which indicates that continuous lighting does not disable stomata (Mortensen and Fjeld 1998; Mortensen and Gislerød 1999; Pettersen *et al.* 2006). In practice, during mild weather periods in spring and autumn it can be difficult to change the vapor pressure deficit (vpd) much by ventilation. Pettersen *et al.* (2007) showed that periodical diurnal temperature variations (between 21 and 27°C) which change vpd were equally effective as a drop in RH at constant temperature for avoiding stomata malfunction of roses grown under continuous lighting.

Continuous lighting of roses is desirable since dark periods are known to enhance the development of powdery mildew (Mortensen and Braut 1998) that is particularly troublesome in greenhouse production of hybrid roses. Studies by Mortensent and Gislerød (2005), Mortensen *et al.* (2007), Pettersen *et al.* (2006) and Suthaparan *et al.* (2010) indicated that severity of powdery mildew was strongly reduced on roses grown under continuous lighting compared with day lengths of 16 h and 18 h. Authors recommend increased day length as an important control measure to decrease powdery mildew in roses. This practice is currently being implemented among Norwegian rose growers. Furthermore, evidence was also found that very low light intensities seem necessary to suppress the fungus (A. Suthaparan, unpublished data). Light-emitting diode (LED) technology is currently developing rapidly, and, in the future, it may be possible to manipulate day length and light qualities with low-energy LED lamps with the purpose of controlling or delaying powdery mildew epidemics (Suthaparan *et al.* 2010). It was reported (Moshkov 1987) that 24-h photoperiod similarly prevented infection of black currant bushes by teliospores of rust fungi, while 100% of plants were infected under 13-14-h photoperiod. The effect of dark period on the development of diseases was probably related to a drop in air/plant temperature followed by a rise in air humidity. Further studies are necessary to clarify the practical impact of continuous lighting as a tool to improve keeping quality of plants in commercial production.

## CONCLUSION

Studies of plant growth and development under continuous light are of current importance as adequate guide-lines for suitable timing, irradiance, spectral energy distribution of the lamps and seasonal use of supplementary lighting for the production of greenhouse crops, transplant production in closed controlled environment systems, the culture of plants in controlled ecological life support systems and *in vitro* production systems require a great amount of knowledge about different crops including their responses to duration of lighting per day. The continuous lighting was found to give benefits to some tolerant crops, which do not develop leaf injuries and can take advantage of the extra light energy provided by continuous lighting. If 24-h photoperiod does not cause adverse effects prolonged low supplementary lighting is often more effective than providing the same light integral at higher rates for shorter periods. The use of a 24-h photoperiod with relatively low PPF was shown to have the benefit of reducing both initial and operational costs for transplant production. However, more research is needed to clarify the practical impact of continuous lighting as a tool to improve post-transplant production and keeping quality of plants. Growing of plants under continuous light may increase yield, but it also increases light energy input per unit biomass produced. Therefore for each particular case the compromise is to be found, especially when planning is to be made for bioregenerative life support systems for space. The use of low PPF has to be a viable alternative when dealing with the low energy constraints.

Due to its ability to accelerate reproductive cycle continuous light was shown to be a useful tool for the breeders of some LD crops as it provides the possibility to obtain several generations of plants in the winter period and ensures more uniform material in respect of developmental rate, time of flowering, leafness etc. compared to shorter photoperiods. For some crops combinations of continuous light followed or preceded by short or long photoperiods depending on plant sensitivity were found to be favorable.

Despite quite a lot of research having been conducted on the influence of long photoperiods on plant growth and development, there is no universal agreement among authors as to the mechanisms involved in the plant response to continuous light and the exact cause of negative effects of continuous light (foliar chlorosis, limited or reduced plant growth and productivity) still remains to be elucidated. It is not clear whether the starch accumulations are responsible for the leaf chlorosis or the light leaf injury observed under continuous light is correlated to photooxidative damage, production of stress ethylene or another processes. The indications are of great interest that plant injury by constant light is not photoperiodic in nature, as shown by the lack of injury under the dim daylength extension treatments and that the injury to plants grown under constant irradiation and temperature is not simply a light response, as shown by the lack of injury under fluctuating temperatures. New research should be undertaken in order to look further into the impact of temperature regimes (day/night differential, temperature drop) on photosynthesis, carbon metabolism and leaf pigment content of plants grown under continuous light. Besides, other growth factors, such as light intensity, light quality, $CO_2$ enrichment, water and fertilizer supply have been reported to have the modifying influence on the effects of continuous lighting. More research are needed to identify the exact causes of negative effects of continuous light on plants and find possible measures preventing physiological disorders in plants caused by continuous daily light periods.

Knowledge on plant growth and development under continuous light can also provide us with better understanding of plant adaptations in the Arctic under conditions of the polar day.

## ACKNOWLEDGEMENTS

The authors gratefully acknowledge that this review has been written with financial support from Russian Foundation for Basic Research (projects 07-04-00063, 08-04-98833, 10-04-00097).

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