Continuous Light as a Way to Increase Greenhouse Tomato Production: Expected Challenges

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Abstract

Tomato plants need six hours of darkness per day for optimal growth; therefore, photosynthesis does not take place for 25% of the day. If tomatoes could be grown under continuous light, a substantial increase in production is expected. In practice, however, continuous light-grown tomato plants develop a potentially lethal mottled chlorosis. Such continuous-light-induced injury is only poorly understood so far. Recently, we proposed a number of hypotheses that aim to explain the continuous-light-induced injury, and rediscovered that wild-tomato species were reported as continuous-light-tolerant. Here, we (i) present a simulation study which shows that if an ideal continuous-light-tolerant tomato genotype is used and no crop adaptations to continuous light are assumed, greenhouse tomato production could be 26% higher when using supplementary lighting for 24 h day^{-1} in comparison with using supplementary lighting only for 18 h day^{-1} during day time, and (ii) discuss expected changes in greenhouse energy budgets and alterations in crop physiological responses that might arise from cultivating tomatoes under continuous light.

INTRODUCTION

In principle, cultivating greenhouse crops under continuous light (CL) should increase yield. This is because by prolonging the photoperiod, the hours per day that plants can fix CO_2 increases. This is a proven concept; for instance, cultivation under CL enhances, to some extent, the growth of lettuce (*Lactuca sativa*) (Arthur et al., 1930; Gaudreau et al., 1994), some potato cultivars (*Solanum tuberosum*) (Wheeler and Tibbitts, 1986) and roses (*Rosa × hybrida*) (Pettersen et al., 2007; Suthaparan et al., 2010). Using CL in production systems ultimately depends on the cost-to-benefit ratio. Considering the high cost of supplementary lighting, only high value horticultural commodities like tomatoes (*Solanum lycopersicum*) could potentially benefit from cultivation under CL.

Continuous light, however, induces negative effects in many plant species, reviewed by Velez-Ramirez et al. (2011). Among all species negatively affected by CL, tomato is particularly sensitive (Arthur et al., 1930; Withrow and Withrow, 1949; Dorais and Gosselin, 1996; Globig et al., 1997; Cushman and Tibbitts, 1998; Demers et al., 1998). The most visible CL-induced negative effects in tomato are leaf chlorosis (Arthur et al., 1930; Withrow and Withrow, 1949; Hillman, 1956; Globig et al., 1997; Cushman and Tibbitts, 1998; Demers et al., 1998) and necrosis (Hillman, 1956; Cushman and Tibbitts, 1998; Demers et al., 1998). The physiological reasons of the CL-induced injury in tomato remain unclear. Recently, by combining previous experimental evidence with the current understanding of plant physiology, we proposed a set of hypotheses that aim to explain the CL-induced injury, and re-discovered that wild-tomato species were reported as CL-tolerant more than 45 years ago (Velez-Ramirez et al., 2011). Modern tools like quantitative trait loci analysis, molecular marker assisted breeding and gene expression profiling should allow the breeding of a CL-tolerant tomato. Although a CL-tolerant tomato genotype is an important achievement, it would not guarantee an increase in greenhouse tomato yield by its own. For that, a better understanding of crop ecology and the mechanism by which CL injures tomato will be also needed. In this paper, we (i) calculate that, for the Dutch winter season, CL could potentially increase greenhouse tomato production by 26% when using an ideal CL-tolerant tomato genotype (a genotype showing no detrimental effects of any kind when cultivated under CL), and (ii) discuss the expected challenges, regarding greenhouse technology and crop ecology, in cultivating tomatoes under CL.

INCREASING GREENHOUSE TOMATO PRODUCTION BY USING CONTINUOUS LIGHT

The potential yield increase that could result from CL was quantified in a simulation study with the tomato crop growth simulation model TOMSIM (Heuvelink, 1999). In these calculations, CL-induced injury and possible physiological and/or morphological crop adaptations to CL are not considered. The model calculates potential production in a pest, disease and weed free environment with ample supply of water and nutrients. The model consists of modules for greenhouse radiation transmission (set at 71% for diffuse radiation), radiation interception by the crop, leaf and canopy photosynthesis, and dry matter production. Maintenance respiration was calculated based on dry mass of 190, 223, 324 and 120 g m^{-2} for leaves, stem, fruit and roots, respectively. In agreement with potential production calculations (Challa and Bakker, 1999), we assumed a constant leaf area index of 3 (90% light interception) and a fixed partitioning to the tomato fruits of 70%; therefore, theoretical maxima were obtained rather than yield predictions. Fruit dry matter content was assumed to be 6.5%. Representative global radiation data for De Bilt, located in the center of The Netherlands, was used as input to the model (Breuer and van de Braak, 1989). Inside temperature was 20°C and a CO_2 concentration was constantly of 700 µmol mol^{-1}. Two supplementary light intensities (200 or 300 µmol m^{-2} s^{-1}) combined with two durations of supplementary light (18 h day^{-1} or CL) were considered; 18 h day^{-1} light implied a 6 h dark period. Lights were continuously on during 18 h or 24 h day^{-1}(CL), also when outside light levels were high.

Compared to 18 h day^{-1} supplementary light (200 µmol m^{-2} s^{-1}), CL resulted in a potential yield increase of 22%. The yield increase was even higher (26%) at 300 µmol m^{-2} s^{-1} of supplementary light (Table 1). This substantial yield increase agrees very well with experimental data obtained by Dueck et al. (2007). These authors applied 162 µmol m^{-2} s^{-1}, between 9 December and 5 April, and observed a yield increase from 13 to 16.7 kg m^{-2} when lights were used 18 h instead of 12 h day^{-1}; these results imply an increase of 3.7 kg m^{-2} as a result of 6 additional hours of supplementary light. Assuming no detrimental effects of CL, therefore, adding another 6 h of light (CL instead of 18 h day^{-1}) would mean a yield increase of another 3.7 kg m^{-2} (20.4 kg m^{-2} in total), which implies a 22% yield increase as founded in this study at a similar light intensity (200 µmol m^{-2} s^{-1}). Using an ideal CL-tolerant tomato genotype, therefore, this study shows that an increase of 26% in tomato production is plausible.

EXPECTED CHALLENGES IN USING CONTINUOUS LIGHT

In The Netherlands by 2005, for instance, the greenhouse industry covered an area of 10,500 ha; about 20% of the greenhouse area was equipped with supplementary lighting. For tomato production, more than 160 ha of greenhouse area were equipped with supplementary lighting (original report in Dutch, cited by Heuvelink et al., 2006). For growing tomatoes under CL, therefore, the infrastructure is already in place. For commercial success of CL-grown tomatoes, however, CL-tolerant cultivars should be bred and the current cultivation practices should most likely be adjusted. Under CL, (i) supplementary lighting, (ii) greenhouse heating and ventilation, and (iii) crop management must be reconsidered. In all cases, plant physiological, crop ecological and greenhouse technological knowledge should guide the adjustments.

Continuous Supplementary Lighting in Practice

Regarding supplementary lighting, which combination of light intensity, light spectral distribution and photoperiod is the best one to use? The advantage of supplementary lighting is higher during winter than during summer (Dorais and Gosselin, 2002); hence, should CL only be used during the winter months? Considering that photoperiods longer that 14 to 18 h day^{-1} induce, to a lesser extent, the same symptoms as CL does (Withrow and Withrow, 1949; Dorais and Gosselin, 1996; Demers et al., 1998), it is expected that CL-tolerant tomatoes will also grow well under photoperiods longer than 18 h day^{-1} yet shorter than 24 day^{-1} (CL). A photoperiod of, for example, 22 h day^{-1} should result in a higher yield since it is significantly longer than the current industry maximum of 18 h day^{-1}, yet a photoperiod of 22 h day^{-1} still gives two hours of darkness to the plants. Then, can higher yields be achieved by cultivating tomatoes under 22 h day^{-1} without having to make too many adjustments in crop and greenhouse management?

The light spectral distribution influences the degree of CL-induced injury (Arthur, 1936; Globig et al., 1997; Murage et al., 1997; Demers and Gosselin, 2002). The light spectral distribution of high pressure sodium (HPS) lamps, which are already installed in some greenhouses, is more or less fixed. However, the potential implementation of light emitting diodes (LED) lamps in greenhouses implies the possibility of managing light spectral quality. Such implementation will post huge challenges since the number of potential lighting regimes will significantly increase. This is simply because LED lighting would allow an independent control of light intensity, photoperiod and spectrum. Having this in mind, testing all the potential lighting regimes would not be feasible. Instead, a fundamental understanding of plant physiology (photosynthesis and photo-morphogenesis) should lead the design of potential light regimes to be used in practice.

Greenhouse Heating and Ventilation under Continuous Light

Nowadays, the increasing human population demands higher yields using fewer resources. Land, water, mineral nutrients and energy are becoming ever scarcer. Therefore, any increase in yield should come with, at least, no decrement in resource use efficiencies. In comparison with open-field agriculture, modern greenhouses are already highly efficient using land, water and mineral nutrients, yet their demand of energy is still large. In a greenhouse situated in northern latitudes, energy is mainly used for heating; in some cases, cooling and supplementary lighting are also used, which also implies energy use. At first glance, therefore, it seems that using continuous light in greenhouses would not only increase tomato yield but also energy consumption. However, it is debatable whether or not cultivating greenhouse tomatoes under CL will decrease energy use efficiency (kg of tomatoes produced per Joule consumed).

For a comprehensive explanation on physical principles of greenhouse climate, the reader is referred to Bakker et al. (1995). In short, the energy balance of a greenhouse depends on all energy inputs and outputs. In temperate climates, the main energy inputs are shortwave radiation and heating; the main energy outputs include latent heat flow, sensible heat flow and longwave radiation. If the energy outputs are high, then the greenhouse should be heated. At night, the vents are closed; therefore, the latent heat loss is negligible. Consequently, longwave radiation and sensible heat flow are the main energy outputs of the greenhouse at night. If the greenhouse is losing, for instance, 100 W m^{-2}, then the heating system should deliver 100 W m^{-2} as well. Usually, those 100 W m^{-2} would come from pipes containing hot water. If the HPS lamps are on, however, an extra energy input would exist. The HPS lamps transform electricity into a combination of shortwave radiation, longwave radiation and sensible heat. The proportion of shortwave radiation that is ultimately converted into carbohydrates is very low (Hall et al., 1999);

according to crop and greenhouse simulations, only about 2% of the annual energy use (including solar radiation, heating systems and CO_2 enrichment) of a greenhouse ends as carbohydrates (Elings et al., 2005). In practice, therefore, the electricity put into the HPS lamps is effectively an energy input that will heat the greenhouse. Hence, when using CL in a greenhouse, the amount of W m^{-2} put into the lighting system would reduce, to almost the same extent, the demand of W m^{-2} that the heating system should deliver. This reasoning suggests that the energy demand of a greenhouse would be the same whether the HPS lamps are on or off; though, this reasoning is likely to be true only if there is no crop in the greenhouse. If a tomato crop is cultivated under CL, the energy demand of the greenhouse is difficult to predict since we are not sure how much a tomato crop would transpire under such abnormal growing conditions. Considering that light induces opening of stomata, a tomato crop grown under CL is expected to transpire more during the night; this would increase the relative humidity in the greenhouse during the night. If there is no active dehumidification, ventilation, with the consequent sensible and latent heat losses, would be the only way to reduce the expected higher air relative humidity. Hence, the energy use efficiency of CL-grown tomatoes would depend on (i) the extent of the expected increase in yield, (ii) the extent of the expected increase in transpiration, and (iii) the combination of greenhouse technologies used. The yield and transpiration of CL-grown tomatoes cannot be accurately predicted yet, as the crop models are not calibrated with CL-grown-crop data.

Greenhouse technologies to be used when cultivating tomatoes under CL are worth discussing. Several sources of heat, electricity and CO_2 exist. Each of those sources conveys different costs and operates at different efficiencies. Two common heat sources are the gas boiler, and the combined heat and power (CHP) generator; they deliver heat and CO_2 or heat, CO_2 and electricity, respectively. Usually during the day, in case of using a CHP generator, hot water is stored in a buffer tank, CO_2 is injected into the greenhouse, and electricity is both used to power the lamps and could be sold to the electricity network; during the night, the stored hot water is used to heat the greenhouse. In a greenhouse with a CL-grown crop, CO_2 and electricity would be also needed at night. Therefore, the CHP generator also should work at night. Additionally, the use of HPS lamps during the night could reduce the demand of hot water; therefore, the CHP generator could deliver too much heat. The possibilities of storing and/or selling extra heat and selling extra electricity could be particularly important determinants in the economic success of using CL in greenhouses. Similarly to the heat, CO_2 and electricity sources, the different ways of reducing air relative humidity, i.e., by ventilation in conventional greenhouses and active dehumidification in closed and semi-closed greenhouses, conveys different costs and energy efficiencies. Although it requires low investment, dehumidification by ventilation conveys large losses in latent heat, sensible heat and CO_2. In contrary, active dehumidification prevents losses of heat and CO_2 to the environment, but the initial investment is large. In addition to the investment and operational costs, regulations will also influence the greenhouse technologies to be used. In The Netherlands, for instance, regulations require screens to reduce light emission from the greenhouse facades to the environment by 95% between 20:00 and 24:00 hours in order to reduce light pollution (Minister van Volkshuisvesting Ruimtelijke Ordening en Milieubeheer, 2002). When screens are closed, heat and water vapor accumulates within the greenhouse; if CL is used, therefore, the greenhouse should be properly equipped to cope with such extra heat and water vapor that cannot be easily ventilated to the environment between 20:00 and 24:00. For cultivating tomato under CL, which combination of greenhouse technologies is the best in terms of costs, energy efficiency and reduction in light pollution? Combining greenhouse climate models and crop models, calibrated with the proper data sets, will help in choosing a combination of technology and management that increases tomato yield without decreasing energy use efficiency.

Crop Management under Continuous Light

To our knowledge, there is no ecological study of a tomato crop grown under CL.

Therefore, the questions regarding crop management are numerous. Tomato yield is determined by assimilates availability (source strength) and the capacity of the tomato fruits to compete for those assimilates (generative sink strength) with the roots and young leaves (vegetative sink strength); in the long term, though, a good balance between vegetative and reproductive growth ensures maximum partitioning to the fruits without compromising future source strength (young leaves) (Heuvelink and Dorais, 2005). Environmental factors and cultural practices influence source and/or sink strengths; for maximum yield, therefore, an optimal combination of light intensity, CO_2 concentration, air relative humidity, water availability, leaf and fruit pruning, plant density and temperature is needed. Under CL, most likely, some of these factors will need adjustments from current optimal settings. CL will provide plants with extra assimilates at night (higher source strength); can the fruits import those extra assimilates, or should the generative sink strength be increased in CL-grown tomato crop? If so, increasing fruit load is a way to increase generative sink strength. If air temperature, air speed, water vapor pressure deficit and stomatal conductance are kept constant, plant temperature will be higher when the HPS lamps are on. If the thermal time concept holds under CL, faster development is expected in CL-grown tomatoes since the plant temperature would be higher during night. A consequence of faster development is higher leaf and truss appearance rates, which implies a shorter growing period for each fruit; this would result in lower average fruit weight. Hence, should the air temperature set point during the night be lower in order to compensate for higher thermal sum in a CL-grown tomato crop?

Diurnal fluctuations in air temperature (thermoperiods) prevent CL-induced injury in tomato plants (Hillman, 1956; Demers and Gosselin, 2002; Ohyama et al., 2005). In principle, therefore, thermoperiods could be used to cultivate CL-sensitive tomato genotypes under CL; nonetheless, it is yet to be proven whether or not a CL-grown tomato crop would have a higher yield, in comparison with a photoperiod of 18 h day^{-1}, when using thermoperiods. As reported by Hillman (1956), fluctuating temperature from 26 to 17°C prevented CL-induced injury; while thermoperiods of 26/20°C did not prevented injury in CL-grown tomato plants. Apparently, a difference of at least 9°C is needed to prevent CL-induced injury in tomato. The optimum temperature for cultivating a greenhouse tomato crop, at the productive stage, is between 19 and 22°C (Peet and Welles, 2005). Such temperature is high enough to achieve almost maximum photosynthesis, yet it is low to reduce as much as possible maintenance respiration, which consumes assimilates without yielding tomatoes. Therefore, the thermoperiods previously found to protect tomato plants from CL-induced injury are too warm. In CL-sensitive potatoes, however, thermoperiods of 14/22°C prevented CL-induced injury (Tibbitts et al., 1990; Cushman and Tibbitts, 1991). Hence, it is reasonable to expect that thermoperiods of 20/11°C would prevent CL-induced injury in tomato plants; to our knowledge, nonetheless, there is no report of CL-grown tomato plants with thermoperods of 20/11°C. Even assuming that thermoperiods of 20/11°C prevent CL-induced injury in tomato, cultivating a tomato crop under CL using thermoperiods would not be extent of potential disadvantages. For instance, low temperatures (around 10°C) reduce specific leaf area (cm^2 leaf g leaf^{-1}), might cause split trusses and malformed flowers, reduce crop photosynthesis, reduce sink strength and might inhibit fruit set because of low pollen viability (Heuvelink and Dorais, 2005). In practice, therefore, would thermoperiods allow a higher tomato production of a CL-grown crop in comparison with current standard practices, while keeping economic and environmental costs low?

The questions continue; for instance, from which developmental stage can growers apply CL in the cultivation? In tomato, CL reduces leaf expansion (unpublished data); this will result in changes in crop canopy and, consequently, in light interception. Smaller leaves will allow deeper light penetration in the crop canopy, which could have a positive effect on overall crop photosynthesis; in order to prevent light reaching the ground, however, a higher leaf area index could be needed. Potential effects of CL over tomato quality should not be overlooked. For instance, CL-grown peppers have increased capsaicin levels (Murakami et al., 2006); will CL change the quality of the produced tomatoes? Answering these questions by detailed crop ecology studies on CL-grown tomato is crucial.

CONCLUSION

Using modern breeding techniques and wild-tomato species, as a source of CL-tolerance, the breeding of a CL-tolerant tomato genotype is plausible. According to crop model simulations, a 26% increase in tomato yield could be achieved assuming no crop adaptations to CL. These results, however, only show the potential of cultivating an ideal CL-tolerant tomato genotype under CL. In practice, it is yet to prove that the CL-tolerance from wild-tomato species is enough to breed an ideal CL-tolerant tomato genotype. Additionally, the simulation study performed here did not consider physiological and/or morphological adaptations to CL, which are likely to occur. To achieve the potential yield increase by using CL, therefore, a detailed study on a CL-tolerant tomato crop is needed; the physiology of the plants, the ecology of the crop and energy-consumption of the greenhouse should be closely monitored. This knowledge is needed to guide the development of crop and greenhouse management techniques for cultivating CL-tolerant tomatoes under CL.

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Tables

Table 1. Simulated tomato fresh yield (kg m^{-2}) from 1 October till 1 April at two intensities of supplementary light and two durations of lighting (photoperiod).

Supplementary light intensity (µmol m^{-2} s^{-1})	Photoperiod ($h\ day^{-1}$)		Yield increase (%)
	18	24	
200	36.0	44.1	22
300	50.8	63.9	26