Photosynthesis and growth at high day temperatures in a CO$_2$ enriched atmosphere

Fotosyntese og vekst ved høye CO$_2$ konsentrasjoner og ulike dag temperaturer

Philosophiae Doctor (PhD) Thesis
Arne Björn Hückstädt

Department of Plant and Environmental Sciences
Norwegian University of Life Science

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Abstract

Increasing energy prices have led to the attempt of energy saving and are one of the main research areas in greenhouse plant production. Technical disintegration has been developed, and the greenhouse concept 'Closed/Semi-Closed Greenhouse' was introduced. The idea of this concept is to reduce energy consumption by cooling the greenhouse under high light intensities, and storing the heat in an underground aquifer to be regained for heating. In order to improve the efficiency of the concept the main focus of this work is investigating how high day temperatures the plants can tolerate at high CO_2 levels without a reduction in photosynthesis or growth.

The average 24 hour temperature is the most important number for the development rate of plants. When day temperatures are high it is therefore desirable to lower the night temperatures. Plants that tolerate high day/low night temperatures will reduce the energy input for cooling in 'Closed/Semi-Closed' greenhouses during the day, and will reduce heating demand during the night.

In this study we used different maximum day temperatures, low and moderate night temperatures, high and ambient CO_2 levels, and manipulation of light quality because high day/low night temperatures lead to shoot elongation. Eight species of herbs, basil (*Ocimum basilicum*), rocket (*Eruca vesicaria*), thyme (*Thymus vulgaris*), oregano (*Origanum vulgare*), lemon balm (*Melissa officinalis*), cilantro (*Coriandrun sativum*), sage (*Salvia officinalis*) and rosemary (*Rosmarin officinalis*) were used for investigating the effect of high day temperature on biomass production and morphology. The tomato varieties (*Solanum lycopersicum* "Mecano", "Capricia", "Cederico") were used to investigate plant response on growth, pollination and fruit development under high day temperatures. The plants were grown in phytotron growth rooms, common greenhouse growth rooms, and gas exchange chambers. When testing the increase of red/far-red light ratio on the elongation of herbs, the plants were covered with a colored plastic film.

The first two investigations were performed by increasing the maximum day temperature stepwise with increasing light intensity while keeping night temperatures steady. The third and fourth investigations were performed using natural increase of maximum day temperature from increasing light intensities, and different but steady night temperatures.

The herbs responded positive to increased maximum day temperatures from 22°C to 29°C with increased dry matter production. An increase of the red/far-red ratio from 1.1 to 10.2

reduced the elongation growth, but also reduced dry matter production due to the 34% lower light intensity below the plastic film.

Increasing the maximum day temperature from 23°C to 29°C under high CO_2 conditions and constant night temperatures did not affect total dry matter production of the tomato plants, but reduced the yield when the maximum day temperature was higher than 23°C, due to a reduction in fruit number and size. Above 23°C maximum day temperature and constant night temperatures a high number of un-pollinated fruits developed. At constant mean day temperature, flowers developed under the highest day and lowest night temperatures (30/11 °C) showed the highest number of pollen and best germination. However, fruits developed under lower day and higher night temperatures (24/17 °C) had a higher amount of soluble solids, dry matter and titratable acid.

The carbon exchange rate (CER) of single tomato plants increased under high CO_2 concentrations with increasing light up to a temperature of 40-45°C. The CER was about 100% higher for plants grown under high CO_2 conditions compared to plants grown under ambient conditions. Chlorophyll fluorescence measurements showed no effect of high maximum day temperatures on the activity of photosystem II. Night temperatures down to 10-11°C showed no negative effect on the CER during the following days and the dark respiration.

The results achieved in this study show that under high CO_2 concentration and high light intensities, the maximum day temperature can be increased and low night temperatures can be accepted without any negative effects on photosynthesis and plant growth. These results can be used in the future to develop strategies with controlled maximum day temperatures in relation to lower night temperatures and combined with CO_2 strategies. They will have great potential for energy saving especially connected to the 'Closed/Semi-Closed' greenhouse concept.

Key words: Carbon exchange rate (CER), chlorophyll fluorescence, closed/semi-closed greenhouse, CO_2 concentration, photon flux density, growth, herbs, light quality, pollen, *Solanum lycopersicum* L., day temperature, night temperature, yield

Sammendrag

Økende energipriser har ført til at veksthusnæringen er meget bevist på å redusere energiforbruket og at energieffektivisering har blitt et sentralt forskningsområde. Tekniske løsninger har blitt utviklet og et nytt dyrkingssystem kalt «lukkede/delvis lukkede veksthus» blitt introdusert. Dette dyrkingssystemet har som mål å redusere energiforbruket ved blant annet å kjøle veksthuset ved sterk innstråling og lagre denne energien for så å bruke den til oppvarming ved behov. For å bedre energieffektiviteten ved dette dyrkingssystemet har en i dette arbeidet undersøkt hvor høye temperaturer plantene kan tolerere ved høy CO_2 uten reduksjon i fotosyntese eller vekst.

Det er den gjennomsnittlige døgntemperaturen som hovedsakelig bestemmer utviklingshastigheten hos planter. Ved høye dagtemperaturer er det derfor ønskelig å senke natt temperaturen. For planter som tolererer høye dagtemperaturer/lave natt temperaturer vil det være et mindre krav til kjøling om dagen ved høy innstråling og redusert behov for oppvarming om natta ved bruk av lukkede/delvis lukkede veksthus.

I dette arbeideidet ble brukt høye dagtemperatuerer, natt temperaturer, ulike CO_2 nivåer og regulering av lyskvaliteten da en kjenner til at høye dag/lave natt temperaturer gir strekningsvekst hos planter. Det ble brukt åtte ulike arter av urter: basilikum (*Ocimum basilicum*), ruccola (*Eruca vesicaria*), timian (*Thymus vulgaris*)*, oregano (*Origanum vulgare*), sitronmelisse (*Melissa officinalis*), koriander (*Coriandrun sativum*), salvie (*Salvia officinalis*) and rosmarin (*Rosmarin officinalis)* for å undersøke virkningen på vekst og morfologi. Videre ble brukt tomat (*Solanum lycopersicum* "Mecano", "Capricia", "Cederico») for å undersøke virkningen på vekst, pollinering og fruktkvalitet ved høye dagtemperaturer. Plantene ble dyrket i dagslysrom i fytotron, vekshusavdelinger eller gassutvekslingskammere. For å teste rød/mørkerødt forholdet på strekningsvekst hos planter ble brukt en farget plastikk.

De to første arbeidene ble utført ved en gradvis økning av den maksimale dagtemperaturen ved økende belysningsstyrke og med faste natt temperaturer. De to siste arbeidene ble utført ved at dagtemperaturen økte naturlig ved økende belysningsstyrke og ved forskjellige natt temperaturer.

Hos urter økte veksten ved å øke den maksimale dagtemperaturen fra 22 °C til 29 °C, mens en i kommersiell dyrking bruker en betydelig lavere temperatur, 13-18 °C. Ved å øke rød/mørkerødt forholdet fra 1,1 til 10,2 ble strekningsveksten redusert, men det førte også til en redusert vekst da plastikken som ble brukt førte til en lysreduksjon på 34 %.

Ved å øke den maksimale dagtemperaturen fra 23 °C til 29 °C ved høy CO_2 og konstant natt temperatur ble det ingen virkning på tørrstoffproduksjonen hos tomatplantene, men en redusert avling ved maksimale dag temperaturer over 23 °C, som skyltes redusert antall og størrelse på fruktene. Maksimale dagtemperaturer over 23 °C og konstant natt temperatur, førte til et økende antall ikke pollinerte tomater. Ved konstant gjennomsnitts temperatur, utviklet tomatblomsterne ved høy dag og lav natt temperatur (30/11 °C) det største antall pollen og med best spireevne. Mens tomater utviklet under midlere dag/natt temperatur (24/11 °C) hadde høyest mengde oppløst tørrstoff, høyest tørrstoffinnhold og høyest titrerbar syre.

Måling av CO_2 opptaket (CER) hos enkeltplanter av tomat ved høye CO_2 nivåer viste at ved økende belysningsstyrke økte fotosyntesen helt opp til 40-45 °C. CO_2-opptaket var dobbelt så høyt for planter dyrket ved høyt CO_2 som ved normalt CO_2 nivå ved disse betingelsene. Målinger av klorofyll fluorescens viste ingen virkning på fotosystem II ved høye dag temperaturer. Natt temperaturer ned til 10-11 °C viste ingen negativ virkning på CO_2 opptaket eller mørke respirasjonen.

Resultatene i dette arbeidet viser at dag temperaturen kan økes betydelig under gode lysforhold og høye CO_2 nivåer. Resultatene viser også at natt temperaturen kan senkes uten at fotosyntesen eller veksten reduseres for tomat. I fremtiden bør disse resultatene kunne brukes for utvikling av strategier for å øke dagtemperaturen ved økende belysningsstyrke og høy CO_2, samtidig som natt temperaturen kan senkes. Dette vil kunne føre til en betydelig energisparing ved bruk av lukkede/delvis lukkede veksthus.

List of papers

This thesis based on the following papers, which are referred to by their Roman numerals

I.   The Effect of High Maximum Day Temperatures and Colored Film Cover on Growth and Morphogenesis of some Herbs in a CO_2 Enriched Greenhouse Atmosphere.
Hückstädt, A.B., Mortensen, L.M., and Gislerød, H.R. 2013
European Journal of Horticultural Science 78 (5): 203-208

II.   The Effect of Maximum Day Temperature on Growth and Yield of Tomatoes grown at high CO_2 level
Hückstädt, A.B., Mortensen, L.M., and Gislerød, H.R. 2013
Submitted to European Journal of Horticultural Science

III. The Effect of High Day and Low Night Temperature on Pollen Production, Pollen Germination and Postharvest Quality of Tomatoes.
Khanal, B., Suthaparan, A., Hückstädt, A.B., Wold, A.B., Mortensen, L.M. and Gislerød, H.R. 2013
American Journal of Plant Sciences 4: 19-25

IV.   Effect of Low Night and High Day Temperatures on Photosynthesis in Tomato.
Hückstädt, A.B., Suthaparan, A., Mortensen, L.M., and Gislerød, H.R.
American Journal of Plant Science - Accepted

1. *Introduction*

The use of growth rooms for plants with glass roofs or walls already started in the 1830's when the 'plant hunters' brought exotic plants from Asia, America and Australia to Europe. The predecessors of the greenhouses were used to protect plants from climate factors outside the greenhouse, like rain or frost (KOPPELKAMM 1981; BOT 1983). Today greenhouses are used to control the climate, to regulate plant growth and quality, production time, and to extend the time of production and becoming independent from season (BOT 1983).

The use of single standing greenhouses for commercial production increased after the industrial revolution in the 19th century, especially due to an increasing demand for vegetables and ornamental plants for the increasing population living in cities. In the beginning of the 20th century the greenhouse production increased all over Europe, and new challenges emerged for greenhouse producers (THORSRUD 1935; BOT 1983). Greenhouse companies in the Northern Latitudes of the world had to face the problem of the poor light conditions during winter time. The use of artificial lighting was not economical at that time, due to high prices of electricity and equipment. Another problem is that winters in these regions are cold, and single glass greenhouses have a bad insulation causing high heating costs (THORSRUD 1935).

The most common combustible was charcoal, but also oil, wood, sawdust, peat and electricity were used to heat the greenhouses. With improvement of oil production, prices for oil decreased and a great number of greenhouses were equipped with oil-fires (THORSRUD 1935). In the last decades prices for crude oil and for oil-borne products increased (BAKKER 1991). Therefore, greenhouse producers are looking for alternative heating fuels, new equipment, and new climate strategies to save energy (VON ZABELTITZ 1982b). Charcoal and biomass (straw and wood), but also natural gasoline, biogas, electricity, solar energy, and heating pumps are used as energy sources for heating (DAMRATH 1982; KLEIN 1982; VON ZABELTITZ 1982a, 1982d).

While the first greenhouses were equipped with single glass, newer greenhouses are covered with a broad spectrum of different materials (VON ZABELTITZ 1982b). Single glass is still used in greenhouse covering, while double glassing is more used today (SCHOCKERT 1982a). To improve transmission, or manipulate diffusion and light quality, different coatings can be applied onto the glass (BRIASSOULIS et al. 1997). Synthetic materials are also used as greenhouse cover, and are available as plastic sheets with a different number of layers,

thickness, and materials. They can contain additives that influence light transmission, light spectrum and diffusion of the incoming light (SCHOCKERT 1982a).

Another improvement in energy saving in greenhouse production is the use of energy saving screens. These screens are often installed between crops and greenhouse cover, and reduce the heat emission under low outside temperature, or reduce the amount of incoming light and heat radiation under high light conditions during summer. These screens can be a simple air bubble film, which is mounted on the greenhouses walls, or it can be an aluminized screen that prevents light entering the crops, thus controlling day length. The plastic screens are made of different materials, and can containing different additives which influence the characteristics of the screen. These screens are generally moveable, and are used on demand (MEYER 1982).

Another possibility of energy saving in greenhouses is the use of climate strategies that reduce the amount of energy used (BOT 1983). These strategies are controlling the conditions inside the greenhouse depending on the climate outside the greenhouse. Under low outside light conditions the temperature inside the greenhouse is increased to the minimum tolerable temperature of the specific plant species. Under high outside light conditions the temperature inside the greenhouse is allowed to increase to the maximum tolerable temperature of the specific plant species, then it is regulated by ventilation (AASLYNG et al. 2003). A computer controls achieved temperatures and adjusts the greenhouse climate to reach the goal of production, instead of using fixed day and night temperatures. Due to the dynamic character of these strategies they are called dynamic strategies, and also include lighting strategies, fertilization strategies, and strategies of CO_2 supply (HEUVELINK and CHALLA 1989; JONES et al. 1991; CHALABI 1992).

Around the year 2005 Dutch researchers developed a climate strategy called 'Closed greenhouse'. The basis for this strategy is that the temperature is controlled by heat pumps, and that no ventilation is used. The temperature is allowed to increase until a certain maximum value before excess heat is removed from the greenhouse by a heat exchanger. The heat itself can be stored in water in underground aqueducts, and be used for heating during the night (OPDAM et al. 2005; HEUVELINK et al. 2008). An advantage of this strategy is that high CO_2 concentrations can be provided to the plants under high light intensities without any loss by ventilation (DE GELDER et al. 2005).

A similar strategy is the 'Semi-Closed Greenhouse', where temperature increase in the greenhouse is partly controlled by a heat exchanger, and the vents are opened when maximum temperature is reached. Due to the lower temperature increase higher CO_2

concentrations could be provided for a longer period, compared to a common ventilation strategy (DE ZWART 2008).

To take advantage of these new climate strategies for greenhouse production, it is important to understand how plant growth is influenced by different climate factors, and how they interact (Figure 1).
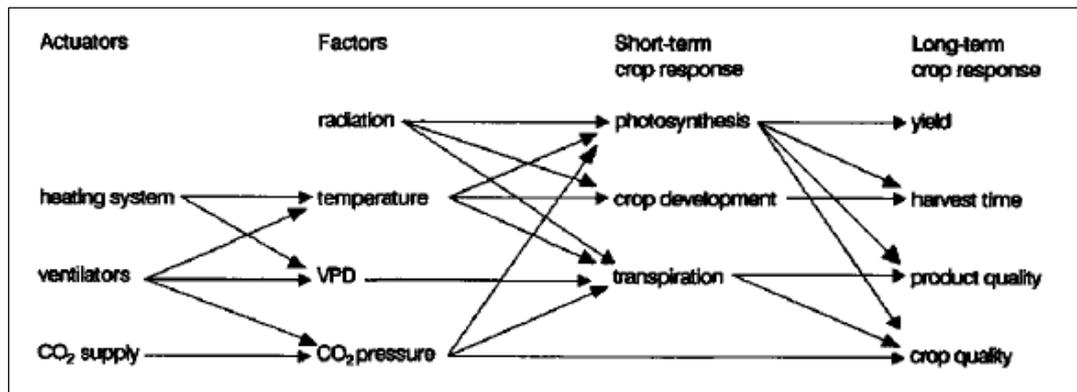

Figure 1. Relations between greenhouse equipment (actuators), climate factors, and the short- and long term response of crops (VPD – Vapor pressure deficit of the greenhouse air)(BAKKER 1991)

1.1. Light in the greenhouse

Irradiation emitted from the sun has wavelengths of 200 to 10000 nm. The irradiation is reflected or absorbed by ozone, dust and water vapor in the atmosphere, so that irradiation of 300 to 2800 nm reaches the soil surface. This irradiation can be split into 7% ultraviolet light (UV light), 46% visible light and 47% infrared light. The UV irradiation covers wavelengths of 200 nm to 380 nm and is further divided into UV-A (315-380 nm), UV-B (280-315 nm), and UV-C (200-280 nm). The visible irradiation (light) covers wavelengths of 380 nm to 750 nm. These can be split into violet (380-420 nm), blue (420-490 nm), green (490-575 nm), yellow (575-585 nm), orange (585-650 nm) and red (650-750 nm). Infrared irradiation covers wavelengths of 750 nm to 2800 nm, which can be divided further into near infrared (750-1400 nm) and short wavelength infrared (1400-3000 nm) (ISO-21348 2007). Infrared radiation is also called thermal radiation, and can be used to measure the temperature of objects. A leaf at 15°C emits an infrared radiation of 7000-14000 nm (STENE 1984).

Light can be quantified in different ways with different physical units. As one possibility, the luminous intensity can be used. The unit is candela, and it describes the wavelength-weighted power that is emitted by a light source in a particular direction per unit solid angle (NATIONAL INSTITUTE OF STANDARDS AND TECHNOLOGY 2000). The measurement is adjusted to the human eye, which can see irradiation only in the visible

spectrum (BASS 1995). Within the visible spectrum the human eye has different sensitivities for different wavelengths, and light in the greenish-yellow wavelength (555 nm) has the biggest luminous intensity compared to other wavelengths (BARTEN 1999). Another way to quantify light is luminous flux/ luminous power. In contrast to luminous intensity that describes the power that is emitted per one unit solid angle, luminous flux describes the power that is emitted in all directions, and both measurements are adjusted to the sensitivity of the human eye. The unit of luminous flux is lumen (lumen). To describe the luminous flux that reaches a specific area the illuminance can be used, it is measured as lumen per square meter (lm m^{-2}) or in lux (BASS 1995). The illuminance is used to describe light in the greenhouse and from artificial light sources. Natural light intensity can range from 0.2 lux, light of full moon during cloudless sky, to 106000 lux during full sunlight and cloudless sky during noon. This measurement is related to the sensitivity of the human eye, and was found inappropriate to describe the light intensity for plants (RIS 1997). To account for plant demand the term photosynthetically active radiation (PAR) was introduced. It covers the part of the spectrum that is used by photosynthetical active species, 400-700 nm, and its unit is W m^{-2}. Due to the fact that light of different wavelengths consists of photons with different energy (blue light has high energy, while red light has low energy), the PAR can only be measured using sensors equipped with distinct filters to adapt for the different energy levels (MCCREE 1981). Based on the stoichiometric relation between absorbed photons and photosynthetic CO_2 binding capacity the measure of the photosynthetic photon flux density (PPFD) was introduced. In contrast to the energy related unit W m^{-2} in the PAR measurement, the PPFD is given in µmol m^{-2} s^{-1}. The latter one is used today as standard in biological studies related to photosynthetic organisms. In literature the terms PAR, PFD (photon flux density) and PPFD are often used interchangeably, and often they have the same definition (FISTRIC 2004).

Light can be the limiting factor in greenhouse production, especially during autumn, winter and spring in temperate climate (CHALLA and VAN DE VOOREN 1980; STENE 1984). During wintertime there is only up to 10% of the light in the greenhouse compared to summer conditions. The primary aim is therefore to increase light transmission through the covering material, and to reduce shading inside the greenhouse caused by construction parts and technical equipment (STENE 1984). The first border the light has to pass on its way into the greenhouse is the covering material. In the first greenhouses glass panes were used as cover. These glasses had a transmission rate of 91-92% while the rest of the light was reflected by the glass surface (SCHOCKERT 1982b). These transmission rates are only achieved when light

impacts on a 90° angle. With decreasing impact angle the amount of light reflected by the glass surface increases. At an impact angle of 45°, 89% of the light is transmitted, at 35° 82% is transmitted and at an angle of 15° only 58% of the light is transmitted into the greenhouse. Those transmission rates are only valid for clean surfaces. Dust, water and algae on the inner or outer surface reduce the amount of light by absorption or reflection by 10-60% (STENE 1984). Single glass has a high thermal conductivity. This led to the development of insulation glass, which consists of two glass sheets that are glued, welded, or soldered, and an inner space of water free air or a heat-insulating gas (CO_2). Such double glassing can decrease the light transmission by 8-25% (SCHOCKERT 1982a; STENE 1984).

Alternatives for glass as greenhouse cover are different kinds of plastic board. These plastic boards can consist of poly-(methyl methacrylate) (PMMA), polycarbonates (PC), or polyvinyl chloride (PVC). PMMA is also known under the trademark of Plexiglas, and is used as single-, double-, or triple wall sheet (SCHOCKERT 1982a). Single layer of PMMA transmit 90% of the solar radiation, a double layer transmits 85%, and a triple layer transmits 75% of the solar radiation. In contrast to glass that partly transmits infrared radiation of 2200-2800 nm, PMMA sheets block all radiation above 2200 nm. Single PVC boards transmit about 85% of the visible irradiance into the greenhouse, and 50% of the infrared radiation from 1700 to 2800 nm (STENE 1984).

Alongside with plastic boards plastic foils are used as greenhouse cover. The most common materials are PVC, polyethylene (PE), and ethylene-vinyl acetate (EVA). Plastic foils of PVC transmit about 95% of the visible light while PE foils transmit about 93-94% of the visible light (VON ZABELTITZ 1982c).

Light is, in addition to CO_2, one of the most important climate factors for plant productivity through the underlying process of photosynthesis. Plants adapt to different light environments by chloroplast movement, changes of leaf anatomy, changes in leaf orientation, and adaptations of the xanthophylls cycle. Only 5% of the energy from sunlight that is reaching the surface of the atmosphere is converted in plant biomass. About 60% of that energy consists of wavelengths below 400 nm and above 700 nm that cannot be utilized in photosynthesis, another 8% are lost by reflection on the leaf surface or by transmission through the leaf, 19% are lost by metabolism, and some of the light is lost by heat dissipation (TAIZ and ZEIGER 2006).

Plant leaf anatomy is developed for maximum light utilization. The first layer the light reaches is the epidermic layer, which is itself transparent to visible light and often convex shaped that it allows focusing the light for underlying cell layers. The second layer of the leaf

is palisade cell layer. It consists of pillar shaped cells that are arranged in columns, and can be up to three cell layers thick. The palisade cells contain a lot of chloroplasts, and are the major cell layer for photosynthesis. In spite of the great number of chloroplasts in these cells some of the light can pass through gaps in between them, or it can be channeled in the central vacuole of the cell or in the free space between cells. The next layer the light has to pass through is the spongy mesophyll layer. It is marked by irregular shaped cells that are connected with large air spaces in between. This structure increases reflection and refraction of the light, thereby increasing the light path through this layer and the absorption rate (NULTSCH 2001; TAIZ and ZEIGER 2006). The composition of these three layers is similar for all leaves, while the thickness of the layers differs. Leaves grown in sunlight are often thicker than leaves grown in shade due to higher number of palisade cell layers and/or longer palisade cells (LICHTENTHALER 1981; LICHTENTHALER et al. 1981). The reason is the lower light intensity in shade, which is less than 20% compared to full sunlight and about 1% in deep shade. Both leaf types are not interchangeable, which means a sun adapted leaf cannot grow under shade conditions and vice versa (TAIZ and ZEIGER 2006). Leaves adapted under shade conditions have a higher amount of chlorophyll base per unit dry weight and also a higher ratio of chlorophyll b to chlorophyll a (LICHTENTHALER et al. 2007), while leaves developed under sunny conditions have more rubisco and a higher pool of xanthophylls cycle components (THAYER and BJÖRKMAN 1990; TAIZ and ZEIGER 2006). Another difference between sun and shade adapted leaves is caused by lower far red light levels in shady conditions. Leaves developed under such conditions often show a higher ratio of photosystem II (PSII) to photosystem I (PSI) ratio, or have a greater number of antenna chlorophyll connected to PS II to improve light absorption and energy transfer (MELIS 1996).

Under low light conditions the upper leaves in a canopy adjust in a 90° angle to the sunlight to receive as much light as possible, while under high light conditions the most upper leaves will increase their position to a much steeper angle to avoid heat damages of the leaf and to let more light penetrate into the canopy onto lower leaves (MC MILLEN and MC CLENDON 1979).

Light response curves are a tool providing information about the photosynthetical performance of leaves. Under low light intensities the carbon dioxide assimilation is negative which means that the leaves release CO_2 as a consequence of mitochondrial respiration. The release is highest under no light conditions, while with increasing light intensity the chloroplasts start the CO_2 fixing process of photosynthesis, so the amount of CO_2 released by the leaves decreases. After a certain light intensity the amount of released CO_2 is in balance

with the amount of CO_2 that is assimilated by photosynthesis. This point is called light compensation point. The compensation point depends on plant species and developmental conditions. Leaves developed under low light conditions reach the light compensation point already at 1 to 5 µmol m^{-2} s^{-1}, while leaves developed at high light intensities reach the light compensation point at 10 to 20 µmol m^{-2} s^{-1}. A reason for this is that shade leaves, as an adaptation to light intensities, have a lower respiration rate, and therefore lower light intensities are necessary to balance the CO_2 release by respiration and the CO_2 fixation by photosynthesis. Increasing the light intensity above the light compensation point is resulting in a linear rise of assimilation in relation to light intensity. At higher light intensities the slope of the graph decreases and the function starts to level off. This point of change is marking the line between light limited CO_2 assimilation, at lower light intensities, and the CO_2 limited CO_2 assimilation at high light intensities. Light intensities above the light saturation point will not increase CO_2 assimilation anymore, because photosynthesis is now depending on electron transport rate, rubisco activity and the metabolism of triose phosphates which is lower than the production of ATP and NADPH by the absorbed light. The light saturation point often reflects the conditions the leaf developed at (STEEMANN NIELSEN and JØRGENSEN 1968; NULTSCH 2001; TAIZ and ZEIGER 2006)(Figure 2).
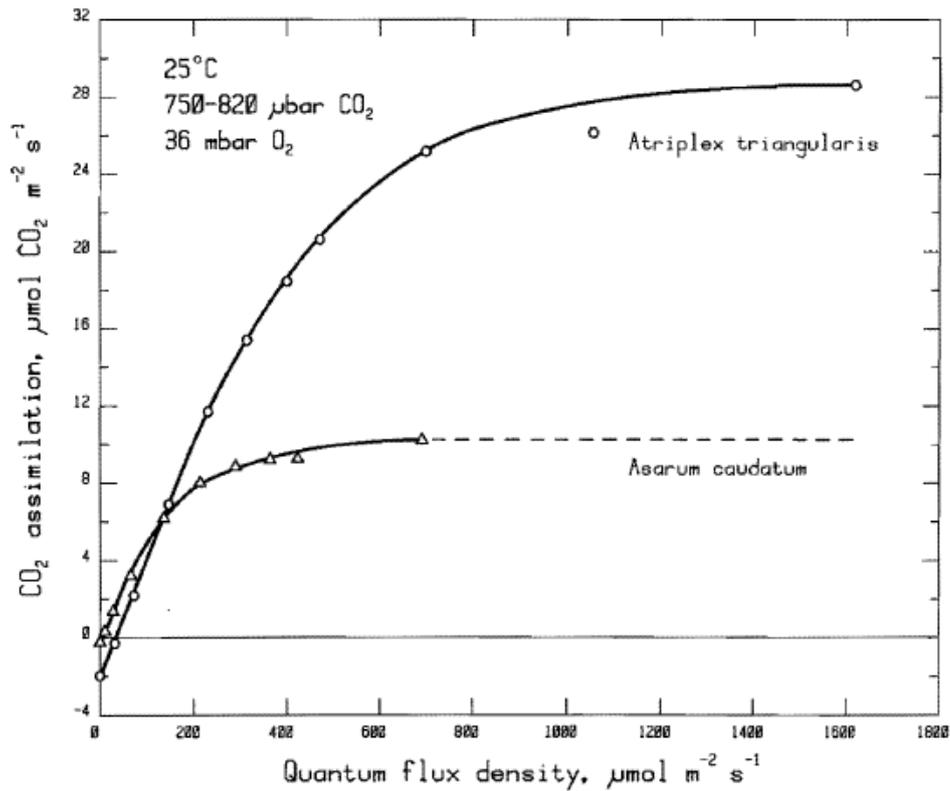
Figure 2. Light-response curve of photosynthetic CO_2 assimilation (μmol m^{-2} s^{-1}) in relation to quantum flux density (μmol m^{-2} s^{-1}) of isolated leaf cells in a sun plant (*Atriplex triangularis*,circle), and in a shade plant (*Asarum caudatum*, triangle). The dashed line has been extrapolated from the measured part of the curve (HARVEY 1979).

The slope of the light limiting part of the graph is reflecting the quantum yield of the leaves, or how many mol of CO_2 are fixed per absorbed quantum/photon. The maximum quantum yield is 0.125 mol CO_2 photon^{-1}, but this value was calculated from biochemical conditions of the chloroplast and cannot be reached in whole leaves. In whole leaves quantum yields are between 0.04 and 0.06 at 380 ppm CO_2 and 21% O_2. The reason for these lower values is the loss of energy through photorespiration in C_3 plants, and the energy demand of CO_2-concentrating processes in C_4 plants. If C_3 plants are treated with higher CO_2 concentration or a lower O_2 concentration the quantum yield can be increased to 0.09, due to lower photorespiration. There is no difference between leaves developed in shade and in sunlight at the same plant, because biochemical processes are similar for both (TAIZ and ZEIGER 2006).

In most plant species the light saturation is at 500 and 1000 μmol m^{-2} s^{-1}, well below the maximum of 2000 μmol m^{-2} s^{-1} of full sunlight (TAIZ and ZEIGER 2006). Since a plant canopy consists of many leaves only a few are exposed to fully sunlight, and often for a short

period of time. Most of the leaves are shaded by others and receive light through gaps in the canopy or by light that is transmitted through other leaves. The photosynthetic efficiency of a complete plant is the sum of the photosynthetic activity of all leaves. As a result, the plant rarely reaches full photosynthetic capacity even in full sunlight (KOYAMA and KIKUZAWA 2010)(Figure 3). ORT and BAKER (1988) showed that under sufficient water and nutrient supply, the more light a crop receives, the higher the biomass production. However, in modern greenhouses plants are shaded under high light intensities to prevent too high temperatures within the crops.
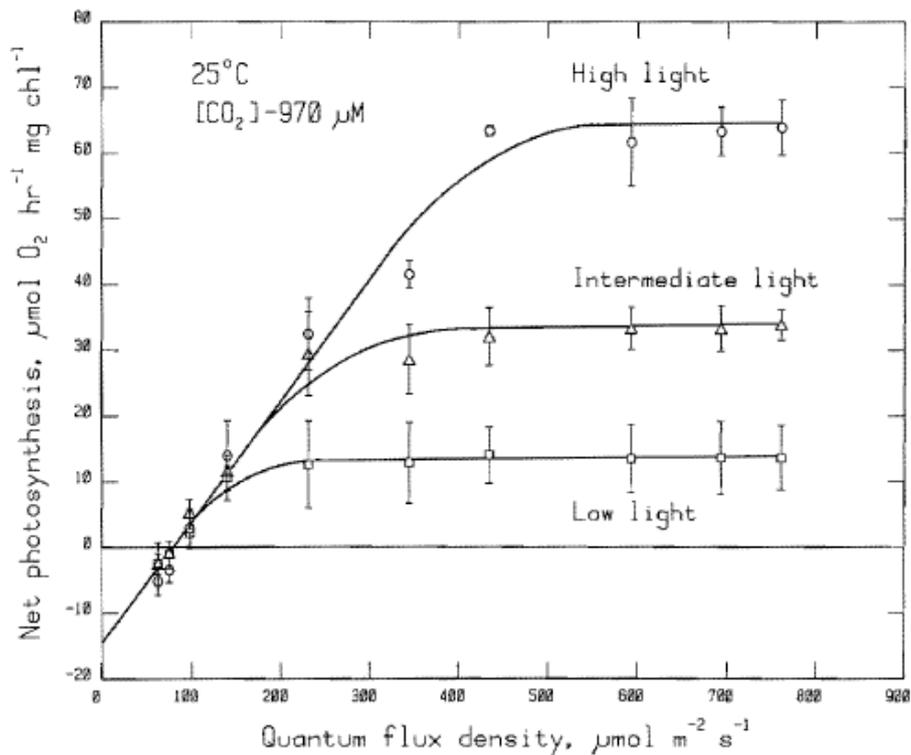
Figure 3. Photosynthetic light response curve of bicarbonate-dependent oxygen evolution (µmol hr^{-1} mg chl^{-1}) in relation to quantum flux density (µmol m^{-2} s^{-1}) of isolated leaf cells from *Atriplex triangularis* grown under conditions of high (44.5 mol m^{-2} day^{-1}; circle), intermediate (14.5 mol m^{-2} day^{-1}; triangle) and low light intensities (6 mol m^{-2} day^{-1}; square). Errors bars indicate the standard deviation. Oxygen concentration was 4-6% (HARVEY 1979)

Under high light intensities the leaves can receive more energy than they can use in the photosynthetical process. Leaves have different possibilities of additional energy removal, which can be non-photochemical quenching, chloroplast movement, or leaf movement as described above (LI et al. 2009).

As a non-destructive method to measure the performance of PSII, chlorophyll fluorescence can be used. The method utilizes the fact that photons hitting a chlorophyll molecule (1) can undergo three different pathways. The photons can drive photosynthesis (2), the energy can be dissipated as heat (2), or it can be reemitted as light (3) (HARBINSON and ROSENQVIST 2003). The latter can be measured as chlorophyll fluorescence.
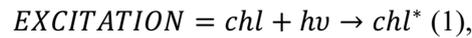
$$EXCITATION = chl + h\upsilon \rightarrow chl^* \ (1),$$
where hυ is a photon, and chl* is an excited chlorophyll in the singlet state
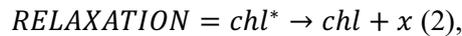
$$RELAXATION = chl^* \rightarrow chl + x \ (2),$$
where x is a product containing the energy of the excited state
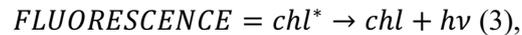
$$FLUORESCENCE = chl^* \rightarrow chl + h\upsilon \ (3),$$
where the energy x is a quantum of energy, represented by hυ

Changes in chlorophyll fluorescence can be measured when light reaches a reaction center of PSII, and the reaction center has already absorbed one electron and is unable to absorb another until the first one is carried onto a subsequent electron carrier. An increasing number of closed reaction centers will decrease the photosynthetic biochemistry and will increase the yield of fluorescence (MAXWELL and JOHNSON 2000).

A sequence for typical fluorescence trace is shown in Figure 4. Parameters achieved from that measurement can be used to calculate the efficiency of PSII, as well as the photosynthetic quenching and the non-photochemical quenching.
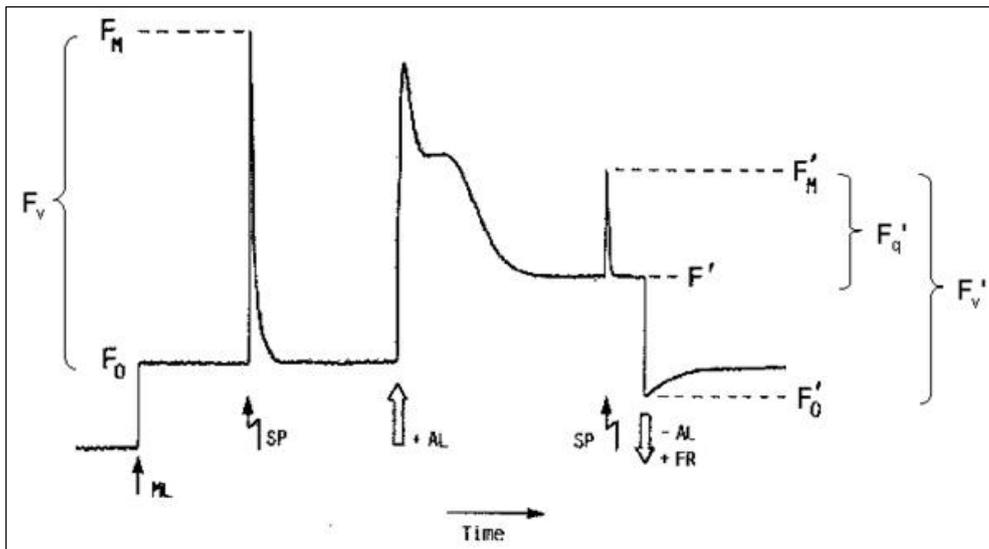
Figure 4. Measurement of chlorophyll fluorescence by the saturation pulse method. A measuring light is switched on (↑ ML) and the zero fluorescence level is measured (F_0). Application of a saturating flash of light (↑SP) allows measurement of the maximum fluorescence level (F_m). A light to drive photosynthesis (↑AL) is turned on. After a period of time, another saturating light flash (↑SP) allows the maximum fluorescence in the light (F_m') to be measured. The level of fluorescence immediately before the saturating flash is termed (F'). Turning off the actinic light (AL), typically in the presence of far-red light (FR), allows the zero level fluorescence 'in the light' to be estimated (VAN KOOTEN and SNELL 1990; MAXWELL and JOHNSON 2000)

Based on the fluorescence trace and the coefficients achieved, photochemical quenching and non-photochemical parameters can be calculated. The most useful parameters that can be calculate for photochemical quenching, are the proportion of the light that is absorbed by chlorophyll associated to PSII, the linear transport rate, the photochemical quenching, and the maximum efficiency of PSII (MAXWELL and JOHNSON 2000).

From the fluorescence trace it is possible to further calculate the non-photochemical quenching, which is part of the photo-protective pathway, and the non-photochemical quenching which is the fastest process, taking only a few seconds to minutes to react. It can be divided into three different components, the state transition, the Δph-dependent quenching, and the photoinhibition, whose task is to dissipate excess energy from high light intensity into heat, thereby protecting the photosynthetic apparatus (MAXWELL and JOHNSON 2000; HARBINSON and ROSENQVIST 2003; SZABO et al. 2005). The state transition, or qT, is a rapid reorganization of the light harvesting apparatus. This process depends on CO_2 availability and the reduction state of chloroplasts. Under inappropriate conditions a system of kinase is activated that is phosphorylating a fraction of the light harvesting complex II (LHCII) protein. The result is a lateral redistribution of the phosphorylated LHCII protein and the associated photosystem I (PSI) (HORTON et al. 2005; SZABO et al. 2005). Photoinhibition is

another part of the non-photochemical quenching and the process is associated to chlorophyll. If light intensity and thereby the energy supply is higher than the energy conversion at the reaction center, the amount of singlet-excited chlorophyll increases. This increase can cause the formation of triplet-excited chlorophyll by intersystem crossing. The high excited chlorophyll can activate molecular oxygen, which then forms a highly reactive singlet state. This reactive oxygen species (ROS) can induce oxidative damage in pigments, proteins, and lipids in the thylakoid membrane, and reduces the photosynthetic efficiency. The process is only slowly reversible or even partly irreversible. Carotenoids remove electrons from the triplet-excited chlorophyll and transmit comprehended energy as heat, which reduces the activation of molecular oxygen, thereby protecting chlorophyll-protein complexes from photo-oxidation (MÜLLER et al. 2001; SZABO et al. 2005). The third component of non-photochemical quenching is the Δph-dependent quenching, or qE. This form of heat dissipation depends on the ph-gradient that arises from photosynthetic electron transport across the thylakoid membrane. Under low light conditions the lumen pH is at about 7.0, and Violaxanthin (Vio) is synthesized from Zeaxanthin (Zea) via Antheraxanthin (Figure 5). When the light intensity increases the pH in the lumen is decreasing, and at a critical threshold the enzyme Vio de-epoxidase is activated which converts Vio back to Zea. The photosystem II S subunit (PsbS) protein plays another important role in qE. This protein contains two acidic residues that are important for sensing the lumen acidification, and it has the ability to bind Zea. Mutants with a lack of PsbS fail for qE, so that protonation of PsbS is the first step in the quenching process, although steps following are unsure (FRANK et al. 2000; SZABO et al. 2005; JOHNSON et al. 2008).
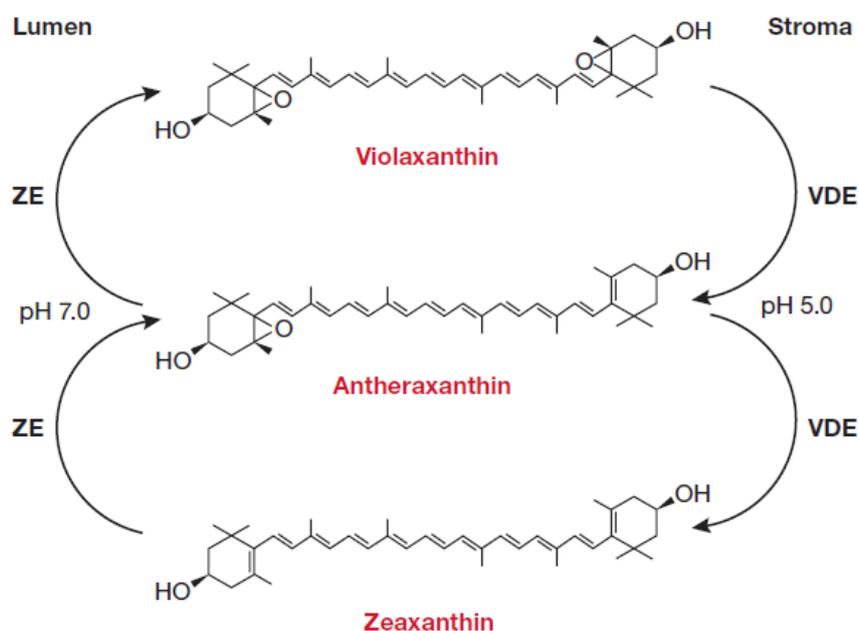
Figure 5. Schematic representation of the xanthophylls cycle showing the de-epoxidation of violaxanthin to zeaxanthin and the epoxidation of zeaxanthin to violaxanthin (VDE –violaxanthin de-epoxidase; ZE – zeaxanthin epoxidase). Both of these reactions occur via antheraxanthin as an intermediate (SZABO et al. 2005).

Another plant strategy to avoid too high energy uptake is movement of the chloroplasts. This process takes a few minutes and is thereby slower than the non-photochemical quenching. Algae, mosses, and leaves of higher plants have the ability to move their chloroplasts within the cells. Under low light intensities the chloroplasts are aligned parallel to the plane of a leaf. In this position they can utilize a maximum of light. If the light intensity increases, and the incoming energy excesses a certain threshold the chloroplasts move along the cells walls and take a position parallel to the incidence light. Hence the amount of absorbed light can be decreased by 15% (KASAHARA et al. 2002).

Apart from the light intensity the light quality is important for plant growth and plant morphology. This process is called photo-morphogenesis. Plants contain different pigments that can absorb different light qualities, and can promote different responses. Two of the most important pigments are the red light absorbing and the blue light absorbing pigment. The red light absorbing pigment is called phytochrome. It is capable to absorb red and far-red light, but also some blue light. The phytochrome exists in two different forms in plants, the red light absorbing form (Pr) and the far-red absorbing form (Pfr). Both forms can be converted into each other by illuminating the particular form with the respective light quality (NULTSCH 2001; TAIZ and ZEIGER 2006).

$$Pr \xrightarrow{\textit{Red light}} \xleftarrow[\textit{Far-red light}]{} Pfr$$
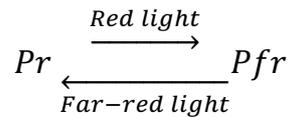
Due to the overlapping characteristic of absorption between Pr and Pfr the pool of phytochrome is never completely converted into one of the forms (Figure 6). Both forms exhibit some absorption in the blue spectrum of light, so that they can be converted into each other by blue light as well. Responses induced by phytochrome are activated by red light, so that the physiological active form is the Pfr (ROCKWELL 2006).
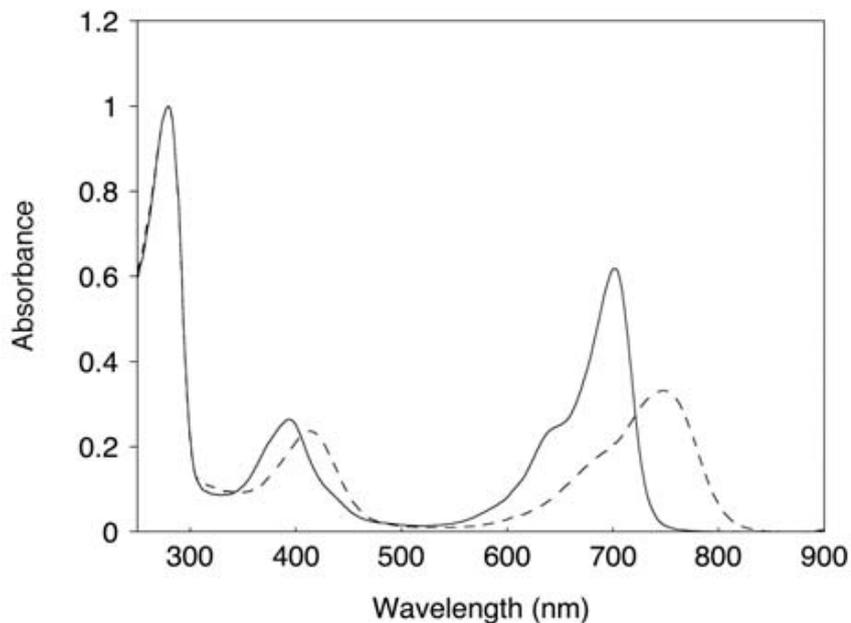
Figure 6. Absorption spectra of phytochrome. The absorption of the red light absorbing state (Pr, solid line), and the absorption of the far-red absorbing state (Pfr, dashed line) (ROCKWELL 2006)

The responses induced by phytochrome can be either biochemical events, or morphological changes. The morphological responses can be observed after a few minutes or after a few weeks. Red light inhibition of stem elongation can already occur after a few minutes (PARKS and SPALDING 1999), while the response of red light on flower induction can occur after a few weeks. Responses that are caused by red light application can be reversed by applying far-red light only for a limited time after initiation of the response, and depend on the number of biochemical actions involved (photoreversibility) (NULTSCH 2001; TAIZ

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and ZEIGER 2006). The response of plants to red light depends on the ratio of red light to far-red light and can be described as:

$$Ratio = \frac{Photon\ fluence\ rate}{in\ 10\ nm\ band\ centered\ on\ 660\ nm} \Big/ \frac{Photon\ fluence\ rate}{in\ 10\ nm\ band\ centered\ on\ 730\ nm}$$

The ratio can differ between 0.13, as it can be measured under a plant canopy, and 1.19, as it can be measured in bright daylight (SMITH 1982). A decreasing ratio will cause stem elongation in plants that developed under sunny light conditions. It will be similar for shade plants, but to a lower extent.

In addition to red and far-red light responses, plants are capable to sense blue light by photoreceptors, and to respond to them. These responses can be phototropism, inhibition of stem elongation, stimulation of chlorophyll and carotenoid synthesis, activation of gene expression, stomatal movement, and the associated enhancement of respiration. The action spectrum for inhibition of stem elongation shows a peak in the red and far-red region that point to phytochrome absorbance, but also a peak in the blue light region of the spectrum (400 to 500 nm). Those two spectra can work independently from each other. In contrast to the response of phytochrome, where a change in the elongation rate is detected after 8 to 90 minutes, a response of the elongation rate on blue light can already be detected after 15 to 30 seconds. In addition to the influence on elongation growth, blue light also impacts the stomatal opening. This is a rapid, reversible effect and targets only the guard cells, and it is a response that occurs during the complete lifespan of a plant (NULTSCH 2001; TAIZ and ZEIGER 2006; RAFFELBERG 2013).

The effect of light on stomatal opening depends on two processes. One of them is a photosynthetic driven process in the chloroplasts of the guard cells, and the other is a process specifically driven by blue light. This blue light response causes the activation of proton pumps that are located in the plasma membrane of the guard cells. The proton pump is a H^+-ATPase, which squeezes protons into the apoplastic space between the guard cells, thus lowering the pH. The grade of acidification depends on the blue light intensity, and acts as a sensor for number of photons reaching the leaf, thereby regulating the width of stomata opening. The evolving pH gradient regulates secondary transport mechanisms which in turn regulate the ion uptake into the guard cells. The most important ion that controls turgor pressure is potassium and its counterions. Guard cells contain about 100 mM of potassium

(K^+) in the closed state, this concentration increases to 400 to 800 mM in the open state, although it depends on plant species and conditions. The potassium in the cells is balanced either by chloride ions (Cl^-) or by malate^{2-}. The pH gradient also generates an electrical component which enables a passive transport of potassium into the guard cells via voltage regulated potassium channels, while chloride is transported via a proton-chloride symporter. Another response that affects osmoregulation of the guard cells which is depending on blue light is the stimulation of synthesis of organic solutes. The main component for this regulation is sucrose. Sucrose is an important osmoregulator mainly in the afternoon, when the potassium level in the guard cells decreases and stomata closure at dusk is controlled by the decreasing content of sucrose. In summary, the osmotic potential of the guard cells can be controlled by uptake of K^+ and Cl^-, the production of sucrose from starch hydrolysis, the production of sucrose by photosynthetic carbon fixation, or by import of sucrose from photosynthetic active mesophyll cells (ASSMANN and SHIMAZAKI 1999; TAIZ and ZEIGER 2006; SHIMAZAKI et al. 2007; RAFFELBERG 2013).

The blue light response on stomata opening can be reversed by giving green light, and can be deemed as analogous to the red/ far-red reversibility. The action spectra for the green light reversal show a maximum at 540 nm and two smaller peaks at 490 nm and 580 nm (FRECHILLA et al. 2000; TALBOTT et al. 2006).

Those facts confirm the importance of light for plant growth and biomass production. To provide sufficient light for plant growth also during periods with low solar radiation, artificial lighting is used in the greenhouses. In the beginning artificial light was used only at low intensities to prolong the lighting period for long-day plants, mainly due to high electricity prices and lamp prices. During that time little was known about the plant's demand on light intensity, light quality and day length (THORSRUD 1935). The first article about long-day and short-day plants was published in 1920 (GARNER and ALLARD 1920). Short-day plants are plants where a certain night length needs to be exceeded for flowering or flower initiation, while in long-day plants the night period needs to go below a certain time, to initiate and develop flowering. A disruption of the night period by light can inhibit flowering in short-day plants, while it can promote flowering in long-day plants (TAIZ and ZEIGER 2006).

Artificial lighting in the 1920's and 1930's was done mainly by using incandescent lamps, although they had an unfavorable spectral energy distribution. In the 1970's the first high pressure sodium (HPS) lamps were introduced to the market, which were more effective

in the transformation of electrical energy into photosynthetic active radiation (PAR) (MOE et al. 2006).
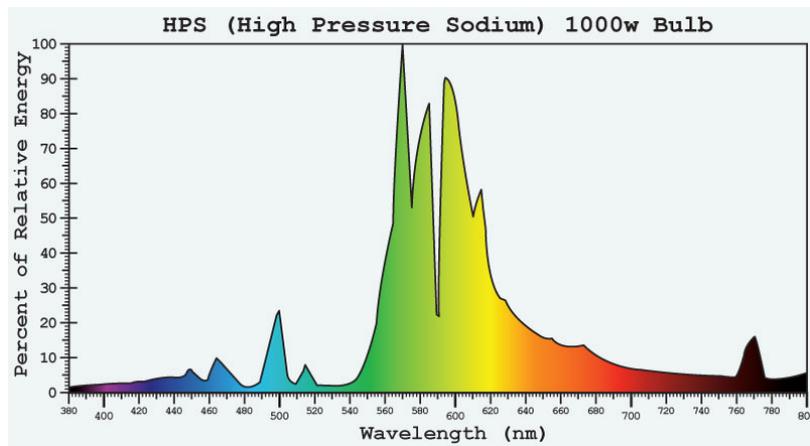
Figure 7. Spectral distribution of a high pressure sodium (HPS) lamp (EYE HORTILUX™; EYE Lighting International, Mentor, OH, USA)

Another lamp type that was introduced to the market in the 1930's is the high pressure mercury lamp. In contrast to the HPS lamp the mercury lamp emits white light with a higher amount of blue and green. The high amount of blue light can induce problems, therefore the light quality was improved by coating the bulb on the inside with phosphorous. High pressure mercury lamps are becoming obsolete from the market due to the better spectral light distribution and higher energy efficiency of metal halide lamps. Those lamps contain vaporized mercury in a mixture with metal halides that improves the efficiency (KANE and SELL 2002)(Figure 8).
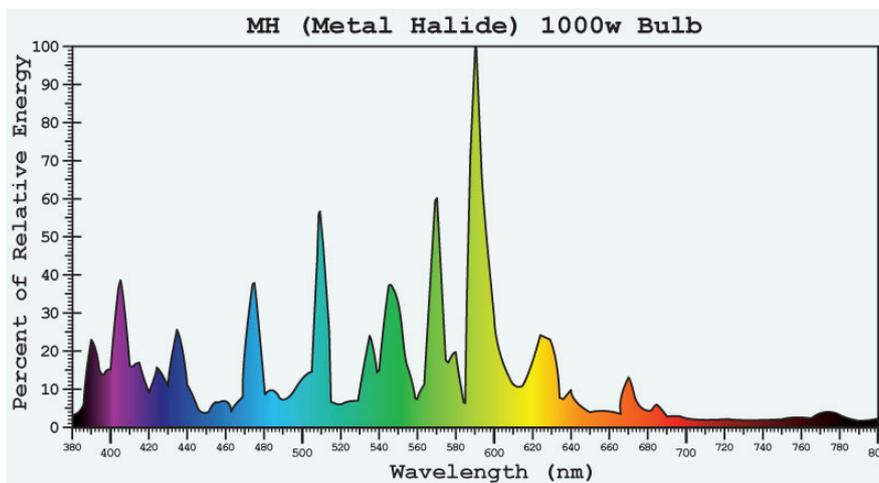

Figure 8. Spectral distribution of a metal halide lamp (EYE HORTILUX™; EYE Lighting International, Mentor, OH, USA)

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A new lamp type that also covers the red part of the light spectrum is the HORTILUX™ BLUE (Figure 9).
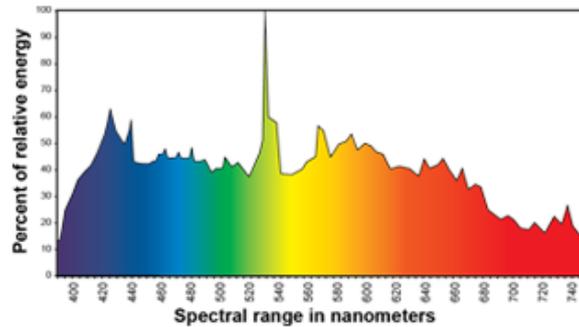
Figure 9. Spectral distribution of a HORTILUX™ BLUE 1000W bulb (EYE HORTILUX™; EYE Lighting International, Mentor, OH, USA)

The specific responses of plants to different light qualities led to the use of light emitting diodes (LED) in plant production. The advantage of LEDs is that they can emit light in a specific wavelength, so that specific responses can be induced. In spite of this advantage LEDs are not used in practical horticulture due to the high cost per unit of light and the demand for a high number of diodes to reach comparable light levels as HPS and metal halide lamps (SHIMOMACI et al. 2006).

With use of light, both from solar radiation or from artificial light sources, irradiation also contains great amounts of thermal energy, and some of the visible light is transformed into thermal energy. This will increase leaf temperature and the temperature in the greenhouse. To avoid temperatures above plant optimum the heat must be removed from the greenhouse, either passively by ventilation or actively by cooling equipment. Another possibility is to prevent thermal radiation to enter the plants, either by shading or by a reflecting coating of the greenhouse cover.

1.2. Temperature in the greenhouse

1.2.1. Air temperature

Greenhouse temperature is the climate factor mainly focused at, because it is one of the most energy demanding factors, and it controls most processes in the plant. Further on, temperature is the most important factor for production timing. The amount of heat that is

accumulated during the growth phase controls physiology, reproduction, and maturity of crops (NAGARAJAN and NAGARAJAN 2010).

To maintain constant temperature in the greenhouse the energy input must balance heat demand and heat surplus. Energy input is provided by heating and infrared radiation from the sun, while energy loss occurs through ventilation, and heat exchange and leakages at the greenhouse cover (STENE 1984). In the beginning of the greenhouse industry the temperature control had to be done manually by opening the vents, that were located on the roof and in sidewalls, and by starting the heating (THORSRUD 1935). Modern greenhouses are controlled by computers that measure the temperature continuously and adjust it by different vent positions or heating following a given scheme. To utilize light and CO_2 concentration in the best way it is important that the plants grow at the optimal temperature for that plant species (BOT 1983). In the beginning little was known about the demands plants have so that for example plants were grown at night temperatures that were 3-6°C lower than the day temperatures, and the day temperatures during summer were higher than during the winter season (THORSRUD 1935). Today we know that the heat demand of plants depend on their biological age, and physical and climate factors. Young plants for example have a higher temperature demand then older plants, and with higher light intensity a higher temperature can be accepted by the plants. This is restricted by the water uptake capacity of the plant and the transpiration rate (CHALLA et al. 2001). In addition, some plant species need lower day temperatures to induce flowers (vernalization) and a higher temperature for flower development, while some species need high temperatures during flower induction and development (SHELDON et al. 2000; TAIZ and ZEIGER 2006).

Night temperature and it's relation to day temperature is also important for plant development as well as for energy consumption. Lower night temperatures mean lower energy input by heating and lower respiration rates, but the temperature decrease is limited by plant species (ADAMS et al. 2011). Plants from tropical regions do not tolerate low night temperatures and can respond with decreased photosynthesis during the next day, while plants from temperate regions accept night temperatures 3-5°C below the day temperature; desert plants can tolerate even lower night temperatures.

High light irradiation often increases the temperature in greenhouse production. By saturation of the CO_2 concentration the optimal temperature increase compare to ambient CO_2 (Figure 10). This enhances the CO_2 assimilation which can be used in greenhouse production. In greenhouses, increasing temperatures can be accepted with increasing light levels, as long the optimal temperature is not exceeded (Table 1).
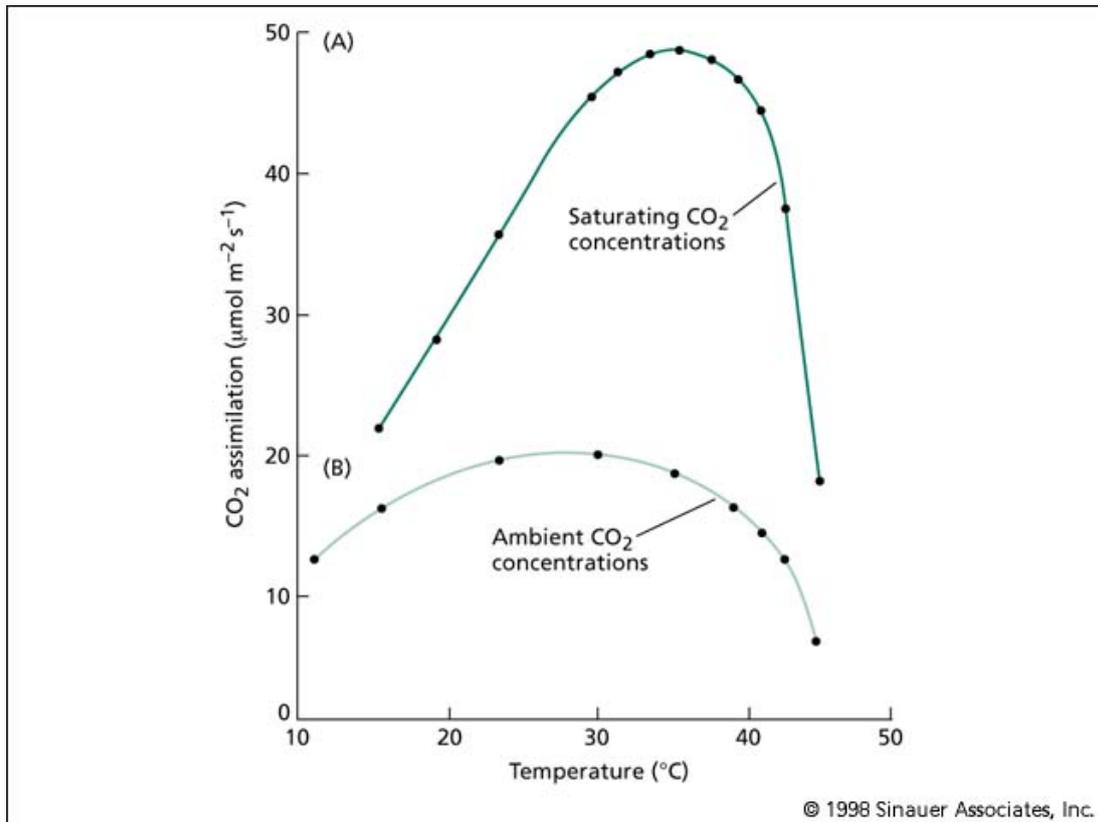
Figure 10. Changes in CO_2 assimilation as a function of temperature at ambient CO_2 concentrations and at saturated CO_2 concentrations. Under high CO_2 concentrations the optimal temperature is higher than under ambient CO_2 concentrations (TAIZ and ZEIGER 2002).

Table 1. Dependency of greenhouse temperature on light intensity in the production of greenhouse tomato (GEISSLER and GOHR 1975).

Light intensity (μmol m^{-2} s^{-1})	Temperature
0 (night)	16°C
0 – 90	17.5°C
90 – 180	19°C
180 – 360	21°C
360 – 540	23°C
> 540	25°C

The morphology of plants can also be controlled by temperature; this is called thermomorphogenesis. Two different factors are important to change the morphology: the average day temperature and the difference between night and day temperature (TAIZ and ZEIGER 2006). The average daily temperature is regulating the formation of new leaves and

the development of flowers. Too high night temperature (>22°C) in Poinsettia (*Euphorbia pulcherrima*) can prolong the time for flower initiation and reduces the shelf life of the cyathia (BÆVRE and GISLERØD 1999). Temperature also influences the elongation of the internode length: high day temperatures increase the length, while high night temperatures reduce the internode length. This response is called thermoperiodism. In this context, the term DIF needs to be mentioned. DIF describes the difference between day and night temperature. The DIF can be either positive, when the day temperature is higher than the night temperature, or it can be negative, when the day temperature is lower than the night temperature. Plants like salvia (*Salvia officinalis*), cucumber (*Cucumis sativus*), and tomato (*Solanum lycopersicum*) show a reduction of internode length when plants are grown under negative DIF. The intensity of this effect is not correlated to temperature difference. Small differences in temperature (1-5°C) can induce a strong inhibition of elongation growth (MYSTER and MOE 1995). A lower day than night temperature requires heating during the night or cooling during the day. This can be an energy demanding strategy, and when natural ventilation is used for controlling the day temperature, an atmosphere with increased CO_2 cannot be established in the greenhouse, thus light use efficiency is reduced (KÖRNER et al. 2004). Therefore often another temperature strategy called DROP is used. In this strategy, the fact that elongation growth is highest when the night turns into day is used. During this period the temperature in the greenhouse is lowered for a few hours, while afterwards a normal positive DIF strategy can be employed. This short drop of temperature in the morning gives similar results in the reduction of elongation growth as a negative DIF, but the effect of DROP depends on the timing, the duration and the amplitude of temperature decrease (MOE et al. 1992; UEBER and HENDRIKS 1992; BÆVRE and GISLERØD 1999). These temperature strategies are influencing the gibberellin pathway in the plant in a way that under negative DIF less physiological active gibberellins (GA_1, GA_3, GA_4) are present, while in plants grown under positive DIF more of the physiological active GA_1 is present. In addition, negative DIF have a similar effect as phytochrome on elongation growth, by reducing the number of cells and the size of the cells in vertical direction (BÆVRE and GISLERØD 1999).

1.2.2.　　Plant temperature

Apart from the air temperature in a greenhouse the plant temperature is important. It can be higher or even lower than the air temperature.

Plant leaves can control their temperature by three processes, radiative heat loss, sensible heat loss, and latent heat loss. The radiative heat loss describes the emission of heat by long wave radiation (above 10 000nm), the sensible heat loss is the transport of heat by air circulation around the leaf if it is warmer than the surrounding air, and the latent heat loss describes heat loss through evaporation of water (transpiration). The sensible and the evaporative heat loss are the most important losses for the leaf, and the ratio between them is described as the Bowen ratio (TAIZ and ZEIGER 2006).

$$Bowen\ ratio = \frac{Sensible\ heat\ loss}{Evaporative\ heat\ loss}$$

Transpiration, and the associated evaporative heat loss of the leaf depends on different factors, for example air humidity. With increasing water content of the air the balance of water potentials is changing. Leaves have a water potential of -15,000hPa, while air has a potential of -1,000,000hPa at a relative humidity of 50%; this potential decreases to -130,000hPa at a relative humidity of 90%. Water flows towards the lowest potential, so the force under low relative humidity is larger than under high humidity. Another factor is the speed of air around the leaf surface. With increased wind speed air is transported away faster and the water potential becomes higher. In calm air a water saturated atmosphere can develop around the leaf which reduces the transpiration rate. Plants take advantage of this fact by developing stomata which are submerged and/or protected by trichome. Furthermore, light intensity influences the transpiration rate due to the fact that under high light intensity the photosynthetic rate increases and CO_2 becomes the limiting factor. Then plants will open the stomata and the CO_2 can enter the leaf, while the plant losses water through the open stomata. An important factor that influences the transpiration rate is temperature. With increasing temperature plants use the coldness that developed under transpiration for cooling the leaves and thus avoid heat damages. With increasing temperature heat absorbed by one transpired water molecule decreases, so that the plant has to transpire more water to keep the same temperature. Another factor is water availability for the plant. In a water deficient plant the xylem stream can be cut and the plant will wilt (STENE 1984; ATV-DVWK 1996, 2002).

The leaf temperature either stays in balance with surrounding greenhouse climate, or it can be below or above the greenhouse temperature. Both situations can cause problems and are tried to be avoided. Under high solar radiation the leaf temperature can be 10-11°C higher than the air temperature, while under open sky conditions in winter, using below-table heating the leaf temperature can be 5-6°C lower than the air temperature. The latter situation can induce condensation on the leaves, which in turn can induce fungal diseases. Important for the leaf temperature during the heating period is the balance of radiant and convectional heat. Radiant heat determines the leaf temperature, and most of it is transformed into convectional heat when a greenhouse is only heated by below-table heating. Therefore a side wall and roof heating is necessary to minimize condensation at the leaves. A common heating pipe emits about 50% radiant heat and the rest is convectional heat (STENE 1984; BAKKER 1991; CAMPEN 2009).

Plant temperature is important for different processes in plant development. Photosynthesis is a process that, in addition to light and CO_2, also depends on temperature. The reason can be seen in the fact that for photosynthesis, chemical processes are involved with a Q_{10} of two or higher. The Q_{10} coefficient is a rate for the temperature dependence of processes and describes the increase of the reaction rate for a temperature increase of 10°C. Temperature independent processes have a Q_{10} of 1, which means that a temperature increase will not affect the reaction rate, while temperature depended processes have a Q_{10} of 2 or higher, which means that the reaction rate will double or increase even more. This dependency is restricted by the minimum temperature, where photosynthesis is still possible, and the maximum temperature where photosynthesis is possible. The minimum and maximum limits depend on the species and can range from temperatures below zero for some varieties of lichens until 70°C and more for cyanobacteria living in hot springs (NULTSCH 2001; TAIZ and ZEIGER 2006). Most field crops show instead permanent wilting at a temperature of 46°C, due to the related high respiration and evapotranspiration rates (NAGARAJAN and NAGARAJAN 2010).

Two processes that influence the photosynthetic rate under increasing temperature are the increasing carboxylation rate (due to increasing speed of chemical processes), and the associated modification in reaction kinetics which leads to a decreasing carboxylation rate, and the lowering of the solubility of CO_2 in water in equilibrium with air, which is higher than for O_2 (Figure 11).
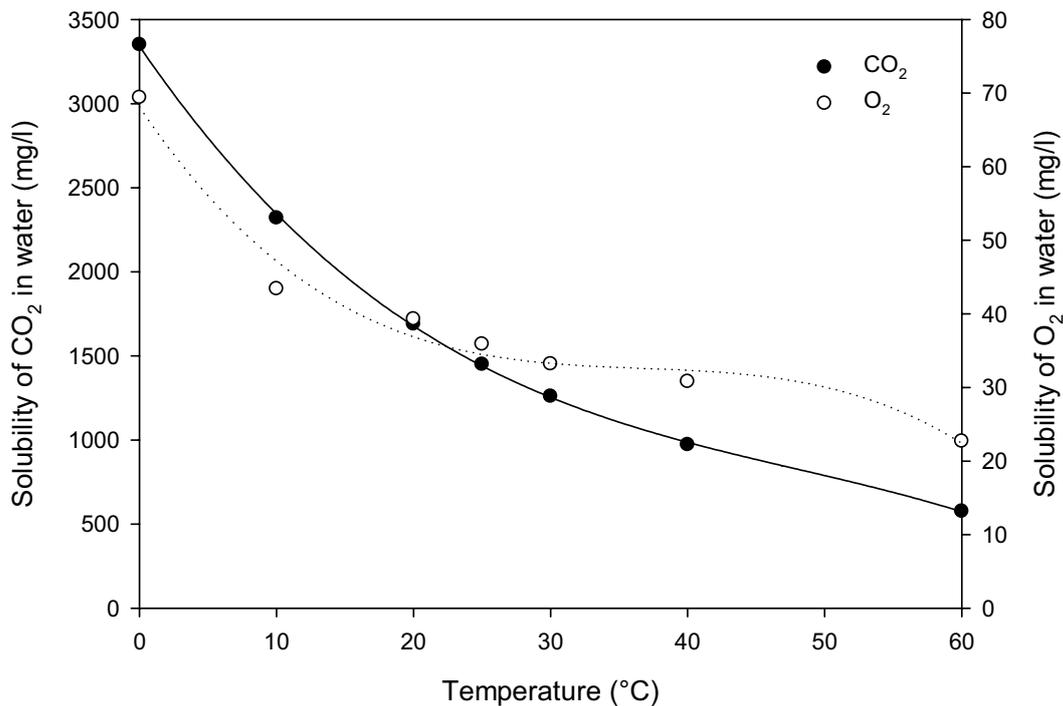
Figure 11. Solubility of carbon dioxide (CO_2) in water (ordinate to the left, black circles, solid line) and solubility of oxygen (O_2) in water (ordinate to the right, open circles, dashed line) in relation to temperature.

Under increased temperature the oxygenation of ribulose 1,5 bisphosphate is increased, which means that instead of two 3-Phosphoglycerates, only one 3-Phosphoglycerate and one 2-Phosphoglycolate are formed. This initiates a chain of chemical reactions that are marked by light-depended O_2 uptake, in connection with a CO_2 evolution in photosynthetic active cells. This process is called photorespiration. An increase in the intercellular CO_2 reduces the photorespiration, due to higher CO_2/O_2 ratio. Photorespiration is just one reason for the decline in photosynthesis under high temperatures, while another is the increasing instability of membrane-bound electron transport processes (BROOKS and FARQUHAR 1985; TAIZ and ZEIGER 2006).

Photosynthesis can also be limited under low temperature. Under this condition photosynthesis is limited by the phosphate content in the chloroplast. Triose phosphates are formed and exported from the chloroplast into the cytosol, simultaneously inorganic phosphate is transported into the chloroplast. Under low temperature starch and sucrose synthesis is reduced, reducing the demand for triose phosphates, thus inhibiting the phosphate uptake into the chloroplast (GEIGER and SERVAITES 1994). Based on this information the photosynthetic response to temperature can be described by a bell shaped curve. The highest

photosynthetic activity can be reached under an optimal temperature, at this temperature all processes are balanced. Above and below this temperature various steps in the photosynthetic process can become limiting. The optimal temperature is related to plant genetics, as well as to environmental conditions the plants developed at; this directs to a broad spectrum of optimal temperatures. These temperatures can range from 0°C for alpine plants to 50°C for plants grown in deserts (NULTSCH 2001; TAIZ and ZEIGER 2006).

1.3.   Humidity in the greenhouse

For humidity in the greenhouse different definitions are used. Water vapor can be quantified either by relative humidity or by vapor pressure deficit. The vapor pressure deficit describes the difference between absolute humidity in the greenhouse air and the absolute humidity of saturated air at the same temperature. The vapor pressure is given in pascal (Pa). One pascal is one newton per square meter ($N\ m^{-2}$). An old unit that was used in former times to describe the pressure was mmHg (millimeter column of mercury), and 1hPa = 100 Pa = 1 mbar = 0.75 mmHg. Another way to describe water content in the air is the relative humidity, which is defined as the ratio between actual partial water pressure in a gaseous mixture of water vapor and air to the saturated water vapor pressure at the same air temperature (STENE 1984). Another way to describe humidity is the absolute humidity, which quantities the amount of water vapor per unit volume ($kg\ m^{-3}$), or per unit mass ($kg\ kg^{-1}$). The difference between absolute humidity and maximum humidity describes the amount of water that can be transpired until the air is saturated with water vapor, and is called saturation deficit (CAMPEN 2009).

Air humidity in the greenhouse depends on the radiation, and thereby on temperature, transpiration, and condensation. In contrast to temperature the humidity is not easy to control. Small changes of a few degrees in temperature can change the air humidity by 10-20%. That is the reason why values for air humidity are given as a range for optimal values, humidity levels below and above can cause problems in the production (STENE 1984). Low humidity levels in plant production can increase the evapotranspiration to a level that causes stress to the plants (BAKKER 1991). One of the stress symptoms is caused by water deficiency, which leads to closure of the stomata, resulting in a reduced gas exchange and thereby reduced photosynthetic efficiency. Too high humidity levels increase the risk of water condensation on the leaves that promote fungal diseases, and high humidity levels can also cause physiological disorders (CAMPEN 2009). In addition, high humidity levels can affect the light interception of plants, by promoting the foliage enlargement (number of leaves, leaf

expansion)(BAKKER et al. 1987; BAKKER 1991) or by a decrease of the leaf area index through calcium deficiency (BAKKER 1990). Calcium deficiency is a nutrient deficiency that often occurs under high humidity levels. It is caused by lower transpiration rates and thereby lower water stream in the plant; as a consequence the calcium (Ca) uptake decreases (BAKKER 1985; DIELEMAN 2008). Ca-deficiency can cause bitter pit in apples, blossom end rot in tomatoes and sweet pepper, tipburn in salad, and leaf yellowing in cucumber. In addition to air temperature inside a greenhouse the covering material of the greenhouse can influence the water content of the air. Depending on the outside temperature and the insulation capacity of the cover water will condensate on the inside, and dehumidify the greenhouse air. This effect will be larger when the difference between outside and inside temperature is large, and the covering material has a high thermal transmittance (U-value, [W m^{-2} K^{-1}]). The factor of dehumidification becomes smaller with better greenhouse cover insulation which also reduces overall energy consumption (VON ZABELTITZ 1982e; STENE 1984).

In some fruiting crops air humidity has an important role in pollination. The pollen sack opens and releases pollen better under dry conditions, while the stickiness of pollen on the stigma and germination is increased under high humidity conditions (BÆVRE and GISLERØD 1999).

1.3.1. *Control of greenhouse humidity*

The control of humidity in the greenhouse is important for plant growth, but also for energy consumption of the greenhouse. An increase of 5% in relative humidity in the control system reduces the demand for dehumidification by 30%, thereby reducing the energy demand by 10% (Table 2)(CAMPEN 2009).

Table 2. Annual transpiration of a tomato crop, dehumidification during heating periods, and the energy consumption needed per square meter of greenhouse under Dutch climate conditions grown under standard conditions (CAMPEN 2009).

Conditions	Transpiration, $l\,m^{-2}\,y^{-1}$	Dehumidification, $l\,m^{-2}\,y^{-1}$	Energy consumption, $MJ\,m^{-2}\,y^{-1}$
Maximum RH 80%	662	158	1459
Maximum RH 85%	640	102	1322

Controlling humidity in the greenhouse is difficult, but there are several possibilities to humidify and dehumidify the air inside a greenhouse.

If the humidity in the greenhouse is too low, it is possible to increase the water content of the air by spraying the plant with water or by watering the plants and/or the tables. In this way up to 10 liter m^{-2} greenhouse area can be evaporated, on a yearly base this can be 500 to 1000 liter m^{-2}. In addition to transpiration from the plants there will be evapotranspiration from the soil, the table, and the ground. This way of humidification costs a lot of energy. Evaporating one liter of water costs about 0.6978 kWh. In a greenhouse of 1000 m^2 this sums up to 697.8 kWh, or about 63 m^3 of natural gas. Some of that energy can be regained from condensation, but most of it is stored in the water vapor in the air. Under high irradiation it can be necessary to spray water on the ground to use the heat loss caused by evaporation for cooling. If water is sprayed on the plants under high irradiation, cooling by evaporation can reduce plant temperature below the air temperature. To increase the air humidity in the greenhouse fogging systems are used. These systems distribute water evenly in the greenhouse by nozzles that produce very fine water drops. The larger the drops, the larger the risk that the water will accumulate at surfaces where diseases might spread from. Under high irradiation and open vents it is more difficult to keep the humidity at a sufficient level, so that spraying has to be done on short intervals (5-15 min) and with short spraying times (2-5 seconds). The amount of water sprayed can vary between some ml and 4-6 liter per 100 m^2 (STENE 1984; BÆVRE and GISLERØD 1999).

If the humidity level exceeds the optimal value it is necessary to dehumidify the air. The common way to do that is by ventilation. Ventilation utilizes the fact that humid air is lighter than dry air. A water molecule has lower molecular weight (18 kg kmol^{-1}) than other gases in the air. On a fixed isobaric volume, evaporating water will replace the heavier nitrogen (28 kg kmol^{-1}), and the heavier oxygen (32 kg kmol^{-1}). Water saturated air of 20°C is 0.9% lighter then dry air (STENE 1984; BÆVRE and GISLERØD 1999; CAMPEN 2009). For ventilation, the vents are opened a few centimeters (5-10 cm) and in addition the temperature of the heating pipes can be increased. An overview over the dehumidification demand in a tomato crop by natural ventilation with and without additional heating is shown in Table 3.

Table 3. Number of hours, maximum dehumidification, and average dehumidification needed with and without additional heating for a single and a double layer (in parentheses) greenhouse for tomato crops, grown with 19/18°C (day/night temperature) between 11th of December and 20th of November. The minimum pipe temperature was 45°C (CAMPEN et al. 2003)

With additional heating			Without additional heating		
Time, h	Max., $g\,m^{-2}\,h^{-1}$	Average, $g\,m^{-2}\,h^{-1}$	Time, h	Max., $g\,m^{-2}\,h^{-1}$	Average, $g\,m^{-2}\,h^{-1}$
1070	145	14	1044	161	8
(1135)	(144)	(34)	(1279)	(163)	(8)

The temperature increase obtained from heating depends on the outside temperature and can vary between 0°C and 45°C, but often it is between 3°C and 15°C. The additional heating for dehumidification costs about 1.56GJ m^{-2} for a single layer greenhouse, and 1.34GJ m^{-2} for a double layer greenhouse. Some of the applied energy is lost as sensible heat under ventilation, which is 74 MJ m^{-2} for a single layer greenhouse and 102 MJ m^{-2} for a double layer greenhouse under tomato crop (CAMPEN et al. 2003). The time it takes until the humidity is lowered depends on the temperature difference between inside and outside, the humidity level inside the greenhouse, and the plants that are grown in the greenhouse. Reducing the humidity in the greenhouse becomes necessary when the temperature decreases. Plants can tolerate humidity levels of 90-95% if the leaf temperature is similar or higher than the air temperature, but if the leaf temperature is lower the risk of condensation on the leaf surface and thereby the risk for fungal diseases increases. Condensation can also occur when the temperature increases in the morning. Thin structures like leaves warm up quiet fast, while thicker structures like fruits need more time, especially at sunrise (CAMPEN et al. 2005).

In closed greenhouses and new greenhouses with a high insulation, the humidity control requires new concepts. In these greenhouses no or very little air exchange occurs between the inside and the outside via ventilation, to keep the greenhouse insulated. The humidity is reduced actively, for example by controlled condensation on a surface with a temperature below the greenhouse dew point; this can be done with and without heat recovery. To induce controlled condensation, surfaces with temperatures of 5°C are necessary. This temperature can be reached either by cooling surfaces with water, or by using a heat exchanger that absorbs latent energy from condensation and sensible heat from the cooling. The gained heat can be stored or used to heat the greenhouse (CAMPEN and BOT 2001).

Another possibility is using a heat exchanger in combination with forced air ventilation. Moist warm air from the greenhouse is blown out, passing the heat exchanger while dry cool outside air is sucked in. In the heat exchanger the heat from the warm greenhouse air is transferred to the dry cool outside air. In this way the system lowers the energy demand that is needed to warm the cooler outside air. The heats that can be regained from the system varies between 30 and 80%, and has a direct relation to the exchanger efficiency (CAMPEN 2009). To gain an even distribution of dry air and temperature, the dry air from outside is distributed in the greenhouse by a perforated film tube, often placed under the crops.

Dehumidification of greenhouse air by condensation on a cold surface would save 0.09€ m^{-2} on a single layer greenhouse, and 0.18€ m^{-2} on a double layer greenhouse, considering a natural gas price of 0.14€ m^{-3}, an energy efficiency of 31.65 MJ m^{-3} gas and a heating efficiency of 95% under tomato crop (CAMPEN et al. 2003). Another active removal of the humidity from the air is the use of hygroscopic material. Hygroscopic materials are often highly concentrated salts (bromides, chlorides), that create a low vapor pressure deficit on their surface due to water absorption, which is the driving force for dehumidification. The latent heat is emitted directly to surrounding greenhouse air, and needs to be removed. The absorbed water has to be removed from the hygroscopic material in a special reconditioning unit, and in addition most of the salts pose a high risk for the environment (CAMPEN and BOT 2001; CAMPEN et al. 2003). Using hygroscopic materials will save 0.44€ m^{-2} in a single layer greenhouse and 0.53€ m^{-2} in double layer greenhouse under tomato crop (CAMPEN et al. 2003).

An invention from Novarbo (Eura, Finland) uses cold water in a curtain as a cold surface to cool the air inside the greenhouse and to remove humidity at the same time (Figure 12). The system is creating a straight vertical curtain of small water droplets, with the water temperature below the greenhouse dew temperature, preferably in the range of 0-15°C. Excess heat and humidity from the greenhouse air will then condensate at the water droplets, which creates airflow, and movement of water within the curtain. Cool and dry air is transported into the greenhouse, while warm and humid air is transported towards the water curtain. In contrast to cooling by fogging systems, the water curtain uses 100-500 liter water per m^2 greenhouse area and hour, although most of the water is recirculated. The cooling capacity of the greenhouse is given as 1 kW electrical energy is transformed into 50-100 kW of cooling power. The warmer water is transported out of the greenhouse and cooled again by

jet coolers that spray the water with fine droplets in big pools, or onto the roof of the greenhouse.
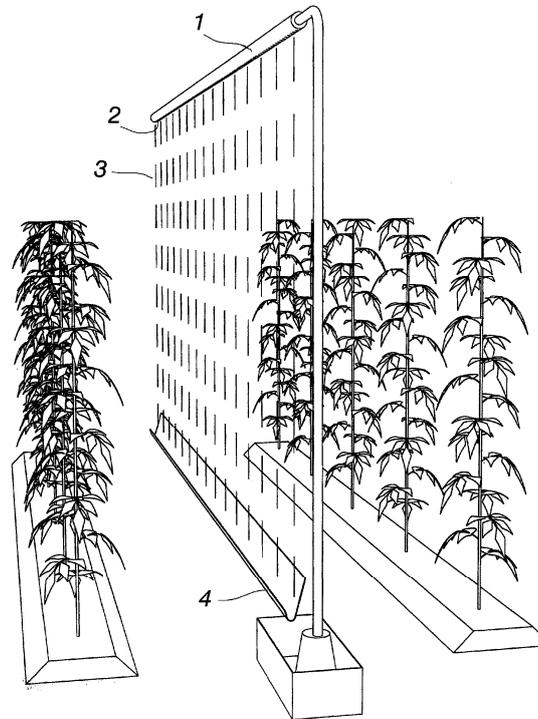

Figure 12. Water curtain as developed by Novarbo (Finland), equipped with adistribution devise (1) where water cooler then the greenhouse dew point is sprayed (0.3-1 mm nozzle holes) (2) between the plant rows. Excess heat and humidity condensates (3) into the curtain and the warmer water is collected in troughs (4) and removed from the greenhouse (US Patent US20090308087 A1).

2.   Objectives of the investigations presented

Increasing energy prices lead to the circumstance that research on energy saving becomes a major task. Energy saving can be achieved by 1. improving the greenhouse equipment, 2. new climate strategies, 3. increasing the production per m^2 production area while using the same amount of energy. In 2005 Dutch researchers introduced a new greenhouse concept which they called 'Closed greenhouse' (OPDAM et al. 2005). The idea of this concept was the combination of an integrated climate concept with a technical system that keeps the vents closed all the time, thus allowing high CO_2 concentrations during the whole lighting period. The 'Semi-closed Greenhouse' is a similar system working with the same concept, but the vents open after the temperature reaches a certain maximum.

The advantages of this concept is the higher yield (20% higher in a tomato production), a reduced demand for chemical crop protection, and a 50% lower use of irrigation water (OPDAM et al. 2005). The disadvantages of the system are high investment costs for a heating pump, an underground aquifer for energy storage, and for an air distribution system. Additionally, the higher humidity in the greenhouse increases the risk for fungal diseases, and costs for cooling the greenhouse under high solar irradiance will increase (HEUVELINK et al. 2008).

In combination with these greenhouse concepts dynamic climate strategies are used for increasing the energy saving potential. In these strategies, the available climate conditioning equipment is used to reach the maximum economic output (VAN HENTEN 1994). Newer models of dynamic climate strategies take photosynthesis and respiration as a base, and the temperature is controlled by the irradiance level. Under low light intensities the temperature in the greenhouse is lowered, while under high light intensities the temperature is allowed to increase. During nighttime lower temperatures can be realized compared to climate strategies with fixed set points (AASLYNG et al. 2003).

The objectives of this study are to further investigate the effects of high maximum day temperatures on plant growth parameters in combination with low night temperatures and under high light intensities and high CO_2 concentrations. The achieved knowledge can be used to supplement dynamic climate strategies used in 'Closed' and 'Semi-Closed' greenhouses with specific minimum and maximum day temperatures under which the yield and quality of the crops is not negatively influenced. These dynamic climate strategies can be used further on to increase the energy saving potential by lowering the energy input during the night due to lower night temperatures. The energy demand for cooling units in a closed

greenhouse will decrease due to possible higher maximum day temperatures. Additionally, an increased plant growth can be expected due to higher CO_2 concentrations during high light intensities, because higher temperatures will reduce the ventilation rate and thereby CO_2 losses.

3.   *Material and Methods*

One of the experiments was conducted with potted plants of basil (*Ocimum basilicum*), sage (*Salvia officinalis*), rocket (*Eruca vesicaria*), thyme (*Thymus vulgaris*), lemon balm (*Melissa officinalis*), cilantro (*Coriandrum sativum*), rosemary (*Rosmarinus officinalis*) and oregano (*Origanum vulgare*). Plants were propagated from seeds in peat, and grown at 22/20°C (day/night temperature), until the first real leaf appeared.

For the other experiments tomato plants (*Solanum lycopersicum* L.) of the cultivars 'Capricia', 'Cederico', and 'Mecano' were used. The plants were propagated from seeds in peat at 22/20°C (day/night temperature) under natural day light conditions. Plants were transferred to experimental conditions when the first flower of the first inflorescence opened.

For the morphological responses of herbs to high maximum day temperature, plants were grown in phytotrone growth rooms with cooling capacities. The herbs were grown at 17°C night temperature and 24°, 28°, 32°, and 36°C maximum day temperatures reached at 800 W m^{-2} global radiation. Temperature increase was 0.9°, 1.4°, 1.9°, and 2.4°C for every 100 W m^{-2} light increase. The rooms were cooled by cool air from below through a perforated floor. The CO_2 concentration in the rooms was set to 880 µmol mol^{-1} during the lighting period and decreased to ambient concentration during the night period. The humidity in the room was set to a vapor pressure deficit of 4.0 g m^{-3} and adjusted by either blowing dry air into the room, or by increasing the humidity with a fogging system. Climate data were measured at plant level and recorded every 15 min. Plants were placed on trolleys (1.5m x 2m) with grids as floor and a plant density of 16 plants m^{-2}. Half of the plants were covered with colored film (Solatrol®, bpi.visqueen Horticultural Products, UK) that increases the red/far red ratio of the light from 1.1 to 10.2. The colored film was placed around the plants, as well as on top of the plants. To ensure a sufficient airflow from the floor to the top a gap of 5 cm was kept between the side and the top of the cover. Subsequent to the experiment, plant height, number of internodes, leaf area, fresh weight and dry weight of the aboveground biomass was measured.

For the effect of high maximum day temperature on tomatoes, the plants were grown in the same phytotrone rooms as the herbs before. The night temperature was set to 16°C, while the day temperature was controlled by sunlight with maxima at 24°, 28°, 32°, and 36°C. The maximum was reached at 500 W m^{-2} global radiation, with a temperature increase of 1.8°, 2.6°, 3.4°, and 4.2°C with every 100 W m^{-2} increasing global radiation. The CO_2

concentration was set to 880 µmol mol^{-1} during the lighting period, while the concentration during the dark period decreased to ambient concentration. The humidity in the growth rooms was set to 85% relative humidity. The experiment was carried out for 6 months and during that time the plants were pruned to 15 to 17 leaves, the side shoots were removed, and the fresh weight and dry weight of the removed parts were measured. The developing fruits were harvested and examined when the color of the last fruit of the un-pruned truss turned from orange to red. The truss weight of the fruits was measured, including the stem, the single fruit weight, the single fruit diameter, and the dry weight of the fruits. At the end of the experiment the plants were harvested and plant height, number of internodes, and fresh and dry weight of the leaves and the stem were recorded.

For the temperature effect on pollen production the plants were grown in greenhouse growth rooms, with 24°/17°C, 27°/14°C and 30°/11°C (day/night temperature). The temperature was allowed to increase with increasing solar radiation until the maximum temperature was reached. High CO_2 concentrations (700µmol mol^{-1}) were provided at times when the vents were closed, while ambient conditions (400µmol mol^{-1}) were provided during night time and during open vents. The air humidity was kept at 75% using ventilation and a fogging system for adjustments. For the determination of pollen production, flowers were harvested and washed in distilled water, and shaken by hand. The number of pollen grains was counted under the light microscope using a haemocytometer. For pollen germination the flowers were shaken above a Petri dish with pollen growth medium. The dishes were sealed and stored at continuous 20°C, 70% relative humidity, and a lighting period of 14h with 130µmol m^{-2} s^{-1} provided by high-pressure mercury lamps. After one day of incubation the number of germinated pollen was counted under the light microscope. Fruits for the postharvest treatment where harvested when fruit color was at a commercial ripening state, using a color chart scale. The harvested fruits where tested for firmness and the color of the fruits was measured using the color chart scale. The fruits were then stored for seven and 14 days in darkness at constant 13°C and 85% relative humidity, before firmness and fruit color was measured. Fruits were further analyzed for dry matter, soluble solids and titratable acid. For this analysis fruits were frozen at -20°C directly after harvest, after seven days in storage and after 14 days in storage.

When studying the effect of low night and high day temperatures on the photosynthesis of tomato, the plants were placed into gas exchange chambers made of 1 mm thick clear plastic with a light transmission of 95%. The chambers had a height of 200 cm and a diameter of 70 cm, with an aluminum ring in the bottom and the top to keep the cylindrical

shape. The chambers were sealed tightly, except for an inlet 5 cm above the ground and an outlet in the top of the chamber. Each of the chambers was equipped with an electromagnetic air pump, which provided the chamber with a defined air mixture and generated an overpressure in the chamber avoiding leakage from outside. The chambers were either provided with air with an ambient CO_2 concentration (400μmol mol^{-1}) or with air with an elevated CO_2 concentration, which were premixed in a separate chamber. The minimum temperature was controlled using three 200W heating elements on the base of the chambers (Figure 3.1). Temperature, light intensity, relative humidity, and CO_2 concentration at the inlet and the outlet were measured continuously and stored every 20 minutes. The measurement of the carbon exchange rate for tomatoes at low night temperatures was performed at tomato plants that were grown under 10°, 13°, 15°; and 18°C night temperature. The plants were either grown under artificial light conditions of 200μmol m^{-2} s^{-1}, or under natural daylight conditions with a day light extension with artificial lighting of 200μmol m^{-2} s^{-1} to provide a photoperiod of 16h. The plants were provided with air of ambient CO_2 concentration during 24h. The humidity in the chambers was not regulated and depended on the transpiration of the plants and the soil. The maximum day temperature in the chambers was not regulated but was set to a minimum of 20°C. To determine the effect of high maximum day temperatures on the carbon exchange rate plants were grown under summer and autumn conditions under natural daylight. The temperature in the chambers was not regulated and depended on the intercepted light intensity. The plants were grown under ambient CO_2 and under elevated CO_2 (1000μmol mol^{-1}) concentrations. For all plants the leaf area, the number of leaves, and the fresh and dry weight of the plants were measured at the end of the experiment. In addition, the chlorophyll fluorescence method was used on plants grown under low night temperatures and on plants grown under high maximum day temperatures, to measure the maximal photosystem II efficiency, the quantum yield of photosystem II electron transport, and the electron transport rate.

Figure 3.1. Gas exchange chambers with tomato plants (Further described in paper 4). Air entered the chamber from an inlet at the base and left at the top. Climate parameters were measured at plant level.

4. Main results and Discussion

The optimum temperature for plant growth increases with increasing solar radiation as well as with increasing CO_2 concentration (WENT 1945; BERRY and BJÖRKMAN 1980; SEGINER et al. 1994; KIM and LIETH 2003), while increasing temperatures often also induce increased elongation growth (GRAY et al. 1998; WEINIG 2000). High temperatures can cause damage in the photosynthetic apparatus (TAUB et al. 2000), or increase the photorespiration (JOLLIFFE and TREGUNNA 1968; BROOKS and FARQUHAR 1985), which can be minimized by giving high CO_2 concentrations (MORTENSEN 1987; TAUB et al. 2000).

4.1. Growth reduction under changed light quality

Increasing the red/far-red ratio from 1.1 to 10.2 by using the colored film reduced slightly the elongation growth in basil by 5%, sage by 10% and thyme by 10%, while in rocket the elongation growth was reduced under low maximum day temperature (MT), but increased under higher maximum day temperature (Paper I). The reduced effects have been described in previous studies (RAJAPAKSE and KELLY 1992; PATIL et al. 2001; STAPEL et al. 2011). Different plant species can vary in their response to a changed red/far-red ratio. MORTENSEN (1990) found no response for increased red/far-red ratio in *Begonia* x *hiemalis*, similar to PATIL et al. (2001) in *Begonia* x *hiemalis* and *Kalanchoe blossfeldiana*. To our knowledge, no results have been published so far showing a changing response of red/far-red ratio under different mean day temperatures, as we could observe in rocket.

Changing the light quality by covers also reduces the amount of light under the cover, due to the absorbing or reflecting character of the cover. The colored film used in this study reduced the light by 34%. This reduction of light caused a reduction in dry weight of basil by 29%, sage by 33%, rocket by 28%, and thyme by 46%. A reduction in dry weight was also observed in chrysanthemum (*Dendranthema* x *grandiflorum* Ramat.), tomato (*Solanum lycopersicum* L.), lettuce (*Lactuca sativa* L.), and petunia (*Petunia* x *hybrid*) when light quality was manipulated by absorbing solutions and selective plastic films (MORTENSEN and STRØMME 1987; RAJAPAKSE and KELLY 1992, 1995; PATIL et al. 2001). The reduction of dry weight was higher compared to the reduction in height, which resulted in weaker and less robust plants compared to the plants grown without the color film.

4.2. Increased maximum day temperature increases dry matter production.

Increasing the mean maximum day temperature increased the dry weight in all of the tested species (paper I). The maximum increase in dry weight was achieved in basil by 36%, in sage by 14%, in thyme by 28% and in rosemary by 22%, when the mean maximum temperature increased from 21.7° to 29.1°C. In rocket and lemon balm the highest increase in dry weight was achieved when the mean maximum day temperature was increased from 21.7°C to 26.2°C by 14% and by 19%, respectively, while in cilantro (16%) and oregano (18%) the maximum increase in dry weight was achieved at mean maximum day temperature of 23.7°C. When the mean maximum day temperature was increased for the latter four, the dry weight slightly decreased but not significantly, with one exception: when cilantro was grown at 29.1°C mean maximum day temperature the dry weight decreased 19% below the weight achieved at 21.7°C mean maximum day temperature. Although the difference between mean maximum day temperatures was high, the difference between mean temperatures was intermediate (from 19.0° to 22.5°C). This may partly explain the relative small increase in dry weight. An increase in fresh weight of basil was obtained by PUTIEVSKY (1983), when the mean temperature increased by 4°C from 24/12°C to 32/12°C day/night temperature under 16h photoperiod. In contrast, FRASZCZAK and KNAFLEWSKI (2009) showed that if the mean temperature is reduced by 5°C from 20/15°C to 15/10°C day/night temperature and 16h photoperiod, basil had a higher fresh weight under the lower temperature conditions; the results were obtained under low light conditions (2.9-3.8 mol m^{-2} day^{-1}). In the study presented a positive response to lower mean temperatures was observed in oregano, which was also reported by PUTIEVSKY (1983), where an increase in mean temperature by 4°C from 24/12°C to 32/12°C day/night temperature under 16h photoperiod decreased the fresh weight.

Tomato plants showed no significant effect of increasing mean maximum day temperature from 23.4° to 29.6°C on the total plant dry weight production (paper II). Similar to the herbs, the difference between mean daily temperatures achieved was intermediate with 2.5°C, and the highest mean daily temperature achieved was 20.1°C, which is below the optimal mean daily temperature for tomato of 25°C (WENT 1944; HUSSEY 1965). In tomato the vegetative growth in terms of total dry weight is more determined by the day temperature than by the night temperature (HUSSEY 1965; HEUVELINK 1989). The developmental rate as well as the early yield of tomato depend on the mean daily temperature, while total tomato yield is promoted by higher night temperatures (DE KONING 1988). Most of the previous research was done with plants grown under ambient CO_2 conditions. Plants in this study had

been grown under elevated conditions, and the achieved results on dry weight are in accordance with resent results of photosynthesis studies in rose and cucumber (MORTENSEN and GISLERØD 2012a; MORTENSEN et al. 2012b). Higher biomass can be expected under high temperature and high CO_2 concentration, due to the promoting effect on photosynthesis.

4.3. Effect of high maximum temperature on tomato yield

Increasing the maximum day temperature, and simultaneously the mean day temperature can increase the developmental rate in tomato (DE KONING 1988) as well as shortening the time for fruit ripening (ADAMS et al. 2001). Increasing the mean day temperature by 12°C decreased the time from flower opening until mature fruits from 95 days under constant 14°C to 42 days under constant 26°C, at elevated CO_2 conditions (1000 µmol mol^{-1}) and 13.6 mol m^{-2} day^{-1} light intensity (ADAMS et al. 2001). However, high fruit temperatures of 38°C can inhibit ripening processes in tomato (LURIE et al. 1996). The total yield of tomato in the study presented decreased when the mean maximum day temperature increased from 23.4°C to 29.6°C (paper II). The reason was a lower number and decreasing size of fruits. These results are in contrast to the results achieved by PEARCE et al. (1993a), who showed a positive relation between increasing fruit temperature in the range of 10°C-30°C and an increase in fruit diameter of 5µm h^{-1} °C^{-1}, at a sufficient water status of the plant (PEARCE et al. 1993b).

Fruits harvested for the present study were divided into fruits with diameters above and below 45mm, which is about 50% of the normal fruit diameter given by the breeder for the cultivars used. Fruits with a diameter <45mm showed no seeds by observation when cut (parthenocarpic). Beside the lack of seeds in these fruits, they showed no further morphological abnormalities, but normal fruit coloring, and normal firmness. The number of fruits with a diameter <45mm increased under increased maximum day temperatures, increasing the yield of those fruits, while the yield of fruits >45mm decreased. The decrease of yield in fruit >45mm outnumbered the increase in fruit <45mm, which resulted in a decrease of total yield. An increase in parthenocarpic fruits was also reported by ADAMS et al. (2001) when the mean day temperature was 26°C, while at 22°C the fruits developed normally. In the study presented the mean day temperature ranged from 17.6° to 20.1°C, and was in the temperature range where ADAMS et al. (2001) reported normal developed fruits. An explanation might be that not the mean day temperature influences the formation of parthenocarpic fruits, but the fruit temperature. In the presented study and in the study of ADAMS et al. (2001) plants received high light intensities that might have led to increase the

fruit temperature above air temperature, and that the inhibiting effect of fruit development and ripening as reported by LURIE et al. (1996) already occurs at lower temperatures.

The achieved total yield for fruits with a diameter >45mm for maximum day temperatures of 23.4°, 26.5°, and 29.6° had been 44.5, 36.3, and 24.0 kg m^{-2}, respectively. Due to the late planting date (21st of April) the harvest started at the end of June until the 3rd of October. Compared with yields of 56.2 kg m^{-2} during a period of approximately 240 days achieved in a closed greenhouse with a maximum day temperature of 26°C under 1000 µmol mol^{-1} CO$_2$ (DE GELDER et al. 2005), the yields in our study were higher for the 96 days of harvest even under the highest maximum day temperature. The reason for the higher yield might be that the trusses in this study had not been pruned, while the trusses in commercial tomato production, for intermediate varieties, are pruned to about six fruits per truss, that a higher number of fruits can develop per truss to increase total yield. The high light intensities and the continuous high concentration of CO$_2$ increased the photosynthetic rate of the plants, providing higher amounts of photosynthetic products, resulting in a sufficient supply for the additional fruits. The harvest index, defined as the ratio of fruit dry weight to total plant dry weight, ranged from 56% under 23.4°C to 36% under 29.6° maximum day temperature. In comparison with previous studies (HEUVELINK 1995) showing a harvest index of 54-60%, the harvest index for the 28° and 32°C MT treatment is lower, while the harvest index for plants grown under 24°C MT is within that range. This difference can be explained by differences in the yield of fruits <45mm, which had been included in the total plant dry weight, but excluded from the fruit dry weight.

4.4. *Pollen production, germination and fruit quality*

Due to the high number of fruits <45mm under increasing maximum day temperature which had been shown to be seedless, it was hypothesized that high temperatures during the day reduces the pollen fitness either by reducing the number of pollen or the germination of pollen. The hypothesis leans also on the results found by SATO et al. (2006), where a moderate temperature stress of 32/26°C day/night temperature reduced the number of pollen released and the germination rate. In the presented study two different maximum day temperatures of 27°C and 30°C were chosen in addition to a control temperature (24°C), to induce high temperature stress in the plants. While the mean day temperatures were similar, the night temperatures were different, to ensure similar developmental rates between the treatments (DE KONING 1988) (paper III).

While keeping a similar mean day temperature, high maximum day temperatures had a promoting effect on the germination rate and number of pollen. Negative effects of the high day temperature might affect pollen germination as well as pollen number as a result of the higher mean daily temperature which was 2.5°C higher in the study presented (paper II) and 4.0°C in SATO et al. (2006). As a side effect under high maximum day temperature the number of abnormal pollen grains increased, but this effect was outnumbered by the increased number of pollen grains released. A possible explanation for the higher number of grains and the better germination rate might be the higher pool of energy reserves in the pollen itself as well as in the plant, due to higher source strength. The photosynthetic capacity in these plants was probably increased, due to higher CO_2 concentration under high light intensities, while the vents were closed to maintain a higher acceptable maximum temperature. The promoting effect of these conditions on photosynthesis has been reported recently for cut roses, cucumber and tomato (MORTENSEN and GISLERØD 2012b; MORTENSEN et al. 2012a)(paper IV). A positive effect of source strength on pollen germinability and number of pollen grains was also reported by FIRON et al. (2006), showing that in heat sensitive cultivars of tomato the starch concentration in the developing grains, as well as the total soluble sugar concentration in the mature grains, was lower compared to concentrations in heat-tolerant cultivars. SATO et al. (2006) and SATO and PEET (2005) instead showed that the major limiting factor for pollen was not the source strength of the plant, but the higher sucrose and lower hexose content in heat stressed pollen grains compared to unstressed grains (SATO et al. 2006).

Fruit quality in terms of total soluble solids, titratable acid, dry matter content, and pH are important factors because they influence the taste, while firmness and fruit color determine the appearance and texture quality in tomato (KADER 2008). Increasing the day temperature increased the total soluble solids content in the tomato fruits due to higher transpiration and changes in the activity of carbohydrate biosynthetic enzymes (BECKLES 2012). Fruits grown at 27°C maximum day temperature had the highest firmness, while there was no difference between fruits developed under 24°C or 30°C maximum day temperature. Storage of the fruits for seven or 14 days decreased the firmness of the fruits, probably due to water loss and decomposing processes.

Dry matter content, concentration of soluble solids, and concentration of titratable acid were highest at 24°C maximum day temperature and decreased when the maximum temperature increased. These results are in contrast to the reviewed results of BECKLES (2012), where increased day temperatures increased the soluble solid content. In the study

presented the night temperature was adjusted to obtain similar mean day temperatures, while in BECKLES (2012) temperature strategies are not described. A higher difference between day and night temperatures might therefore have a greater impact on fruit composition then increased day temperatures. Dry matter content, concentration of soluble solids, and pH were not affected during storage, while the concentration of titratable acid decreased. Similar results were achieved by AUERSWALD et al. (1999) and JAVANMARDI and KUBOTA (2006). But most of the research done on the amount of soluble solids has looked at them as one factor, while in addition to sugars they also consist of organic and amino acids and soluble pectins, among others. Reports of soluble solids being unaffected by storage and storage temperature have to be viewed with caution, because individual sugar contents were often not measured. GÓMEZ et al. (2009) showed that tomato fruits had about 25% less glucose when chilled under storage at 15°C compared to fruits stored at 20°C.

4.5. *Carbon exchange rate (CER) at low night and high day temperatures*

Increasing the maximum day temperature can have negative effects on the photosynthetic capacity of plants, due to higher photorespiration and heat damages on the photosynthetic apparatus. Both effects can be minimized by increasing the CO_2 concentration in the greenhouse to 500-1000 µmol mol^{-1} (MORTENSEN 1987; TAUB et al. 2000), because the optimal temperature for photosynthesis increases with increasing CO_2 concentration and light intensity (BERRY and BJÖRKMAN 1980; KIM and LIETH 2003). Low night temperatures instead can decrease the dark respiration rate and cause end-product assimilation in the leaves, thus reducing photosynthetic capacity during the following day, especially in long dark periods with low temperatures in combination with low day temperatures (PAUL and FOYER 2001; HEINSVIG KJÆR et al. 2007). Growing whole tomato plants in gas exchange chambers showed no negative influence on the CER during the night, or on the CER during the next day (paper IV). Plants in that study were grown at 23°-25°C day temperature and the lowest night temperature was at 10°C. Most earlier studies on the inhibiting effect of low night temperature on dark respiration and CER in the light, were done either at very low night temperatures, 4°C in MARTINO-CATT and ORT (1992), or at a combination of low night temperatures with low day temperatures, 16/14°C day/night temperature (VENEMA et al. 1999).

During summer, light conditions achieved in the gas exchange chambers were close to the maximum light intensity (about 1000 µmol m^{-2} s^{-1}) which increased the temperature inside the chambers to 40°-45°C. The CER rate of the plants increased as long as the CO_2

concentration inside the chambers was kept high. Plants grown under ambient CO_2 conditions reached the maximum CER at a lower photosynthetic flux density (PFD), although a further increase in temperature did not decrease the CER. These results are in accordance to recent results obtained for cut roses and cucumber (MORTENSEN and GISLERØD 2012a; MORTENSEN et al. 2012b). The results indicate that high temperatures of 40°C and above in tomato do not affect photosynthesis negatively when the CO_2 concentration is kept high and the plants receive high light intensities. In contrast, CAMEJO et al. (2005) reported that a heat shock of 45°C for 2h reduced net photosynthetic rate of about 50% in a heat-sensitive tomato cultivar, but the authors did not report the CO_2 concentrations the plants had been grown at and the gas exchange was measured at 350 µmol m^{-2} s^{-1} PFD. The plants in the study presented had been exposed to high temperatures only for a short period of time (measurement was performed every 20 minutes), so that the 2 hours used by CAMEJO et al. (2005) might be a critical time span to inhibit photosynthesis. GEORGIEVA (1999) reviewed that heat damages of the photosynthetic apparatus depend on the light intensity as well as on the duration of high temperature. Another point is that most of the research conducted on photosynthesis in plants has been done using leaf cuvettes on single leaves either attached or detached to the plants or on leaf disks. Just a few reports have been published measuring the carbon exchange rate in complete plants (NEDERHOFF and VEGTER 1994; KÖRNER and CHALLA 2003; KÖRNER et al. 2007). This is important because PERCIVAL et al. (1996) found that complete plants have a lower sensitivity for high temperature compared to single leaves.

Measurements of chlorophyll fluorescence on dark adapted leaves in the study presented showed no effect of low night temperatures on the maximum quantum yield of photosystem II (F_v/F_m), and neither an effect of high day temperatures nor CO_2 concentration on F_v/F_m, electron transport rate (J) and the efficiency of photosystem II (Φ_{PSII}). CAMEJO et al. (2005) reported a significant reduced F_v/F_m and reduced Φ_{PSII} for heat-sensitive plants after heat shock treatment, while a heat-tolerant variety showed no response in either of them. The maximum temperature for detectable electron flow rate was reported as 45.3°C (SMILLIE and GIBBONS 1981), while the activity of photosystem II decreases above 38°C (MURKOWSKI 2001). No reports have been found that characterized the studied cultivar 'Mecano' as a heat-tolerant variety.

5. General Conclusions and Further Perspectives

- Increasing the maximum day temperature in the tested herbs species had a positive effect on the dry matter production, although not all species tolerated the highest temperature.

- Using color plastic film (Solatrol®) as a cover reduced the elongation growth but also decreased dry matter production to a high extend, resulting in weaker plants.

- Increasing the mean day temperature did not affect dry matter production in fruiting tomatoes, but decreased number and size of the fruits, thereby decreasing the yield.

- A higher difference between night- and day temperature increased the number and germination rate of tomato pollen, when the mean day temperature was kept the same, and fruits grown under a lower day/night temperature difference were of higher quality.

- With temperatures up to 40-45°C the photosynthesis was twice as high with elevated CO_2 compare to ambient

- Low night temperatures (10°-11°C) and high day temperatures (40°-45°C) had no negative effects on the CER in tomatoes, and did not affect the activity of photosystem II.

Researches of greenhouse climate effects on plant growth are revealing a great complexity of the involved processes, and manipulation on one climate factor influences other factors as well.

Results from paper I show that there are differences between different plants species in the performance under high maximum day temperature, but there also might be differences within species depending on the genetic origin of the cultivars.

Further research is necessary to find out how tomato plants will respond when high temperature amplitudes are applied to the plant during a complete season. Important factors here are the impact on vegetative growth, for itself and in relation to generative growth, and the impact on fruit development and yield.

In this study the experiments were performed mainly in summer and autumn, so that additionally the influence of high temperature amplitudes during the day and lower light conditions on the humidity in the greenhouse need to be investigated in relation to plant growth and fungal diseases.

High maximum day temperatures may also influence the developmental rate of pests and their biological predators, or might influence the activity and development of pollination insects, which then might result in lower pollinations rates.

The measurements for carbon exchange rate were done on single plants, each exposed to utilize the maximum amount of light. Further research is needed on plants grown within a plant canopy, to take shading effects of neighboring plants into account, as well as the influence of ripening fruits as carbon sink at the plants.

The results for tomato yield in paper II indicate that higher yields are possible under new temperature strategies compared to common strategies, and in combination with the results from paper III the number of un-pollinated fruits might decrease under higher day and lower night temperatures. The results from paper IV indicate no inhibiting effect of high day and low night temperature on CER, so a higher number of fruits per truss seems possible. This needs to be examined for its practical application.

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Paper I

The Effect of High Maximum Day Temperatures and Coloured Film Cover on Growth and Morphogenesis of some Herbs in a CO_2 Enriched Greenhouse Atmosphere

A. B. Hückstädt, L. M. Mortensen and H. R. Gislerød
(Department of Plant and Environmental Sciences, the Norwegian University of Life Sciences, Ås, Norway)

Summary

The effect of different maximum day temperatures (21.7, 23.7, 26.2 and 29.1 °C) was studied in basil, sage, rocket, thyme, lemon balm, cilantro, rosemary and oregano in CO_2 enriched (800 µmol mol⁻¹) day-light phytotron compartments. In addition, four of the species were covered with coloured plastic film in order to control plant morphogenesis (increased ratio of red/far red light). The dry weight of all species responded positively to maximum temperatures above 21.7 °C, cilantro and oregano up to 23.7 °C, basil, rocket and lemon balm up to 26.2 °C, and sage, thyme and rosemary up to 29.1 °C. The plastic film reduced the dry weight of basil, sage, rocket and thyme by 29–46 % due to a 34 % reduction in photosynthetically active radiation. In general, it was concluded that higher temperatures than those normally used should be applied in order to increase growth. The use of coloured plastic film to control morphogenesis, however, reduced plant growth and appeared to be of no practical benefit.

Key words. closed greenhouse – CO_2 concentration – *Coriandrum sativum* – day light – *Eruca vesicaria* – light quality – *Melissa officinalis* – temperature – *Ocimum basilicum* – *Origanum vulgare* – *Rosmarinus officinalis* – *Salvia officinalis* – *Thymus vulgaris*

Introduction

It is generally recommended that herbs are grown at 13 to 18 °C, and high day temperatures should be avoided (Gibson et al. 2000; Lasseigne et al. 2007). The CO_2 concentration used is often not reported in studies on herbs, or, in the event that it is, CO_2 enrichment has not been applied. In addition to the amount of photosynthetic active radiation (PAR), the CO_2 concentration might significantly influence the temperature response of plants (Mortensen and Gislerød 2012). Low outside temperatures or the use of active cooling inside the greenhouse will reduce the need for ventilation during the day, and a high CO_2 level might thus be maintained (Qian et al. 2011). If a cheap source of CO_2 gas is available allowing large amounts to be used (> 50 kg 1000 m⁻² h⁻¹), a high concentration can be maintained irrespective of ventilation (Qian et al. 2011). Relatively few studies have been done on the temperature effect on herbs. Using a fixed night temperature of 17 °C, we therefore wanted to evaluate the effect of different maximum temperatures on a range of herb species in a CO_2 enriched environment. It is well known that large temperature fluctuations between day and night often stimulate shoot elongation that can be negative for herbs (Erwin et al. 1991; Myster and Moe 1995). Some of the herbs were therefore covered with a coloured plastic film that significantly increased the red/far red ratio of the daylight. This type of change in the red/far red ratio is known to strongly reduce shoot elongation (Mortensen and Strømme 1987; Rajapakse et al. 1999). Bearing in mind that the plastic film reduced PAR by 34 %, we wanted to evaluate the effect of such selective light absorbing films in practice in Scandinavia.

Material and Methods

Seeds of basil (*Ocimum basilicum*), sage (*Salvia officinalis*), rocket (*Eruca vesicaria*), thyme (*Thymus vulgaris*), lemon balm (*Melissa officinalis*), cilantro (*Coriandrum sativum*), rosemary (*Rosmarinus officinalis*) and oregano (*Origanum vulgare*) were sown in 12 cm pots with peat (Veksttorv, Ullensaker Almenning, Nordkisa). Sage, rosemary and cilantro seeds were covered with vermiculite. All the pots were covered with white/black plastic until germination. After germination, the number of plants was reduced to 20 per pot. The day/night temperature during germination was 22/20 °C. Supplementary light was applied to

the seedlings at a photon flux density (PFD) of 100 µmol m^{-2} s^{-1} (high pressure sodium lamps) when outside global radiation fell below 440 µmol m^{-2} s^{-1} during the photoperiod of 14 hours (h). A complete nutrient solution with a conductivity of 1.8 mS cm^{-1} (a 50/50 % mixture of Superba Red and Calcinit, Yara, Norway) was applied daily.

When the seedlings developed their first true leaf, the pots were transferred to four phytotron compartments with daylight only (at the Centre for Plant Research in Controlled Climate) in Ås, which is situated at latitude of around 60° N in Norway. The experiment was carried out from 17 August until 11 September, and repeated from 12 September until 2 October, 2009. The day length changed from 14 to 11 h during the experimental period. The PAR at plant level was 13.4 ± 1.1 and 11.2 ± 0.7 mol m^{-2} day^{-1} (mol m^{-2} d^{-1}) in the two periods, respectively, and for the whole experimental period 12.2 ± 0.7 mol m^{-2} d^{-1}. This was 50 % of the radiation outside the greenhouse. The night temperature was 17.2 ± 0.2 °C for all four treatments, while the day temperature was controlled by the solar radiation. With every 100 W m^{-2} increase in global radiation the air temperature increased by 0.9, 1.4, 1.9 and 2.4 °C up to maximum temperatures (MT) of 24, 28, 32 and 36 °C in the four compartments, respectively. The MT was reached at 800 W m^{-2} global radiation (1800 µmol m^{-2} s^{-1} PFD). Since the radiation did not reach 800 Wm^{-2}, the respective maximum temperatures were never actually reached. The mean and maximum temperature as well as the vapour pressure deficit (VPD) and CO_2 concentration (representing both experimental periods) are shown in Table 1 and a representative climate record during eight days in Fig. 1. A time delay of ten minutes was used in the temperature control system in order to avoid frequent temperature changes due to varying cloud cover. The air humidity set point was 80 % relative humidity (RH) in the four growth rooms and was controlled by a fogging system. At the highest temperatures the fogging system was not able to keep RH at this level and could decrease to around 60 % RH (Fig. 1). The mean VPD for the four treatments are given in Table 1.

The plants used in the experiment were divided into two groups, one with daylight only and one covered with a coloured film (Solatrol®, bpi.visqueen Horticultural Products, UK). The plastic film increased the red/far red ratio of the daylight from 1.1 to 10.2 (SKR 110 660/730 Sensor, Skye Instruments Ltd, UK). The cover reduced the light level by 34 % (Sky instrument, Model EPP2000C-100, StellarNet Inc., Tampa, FL, USA). Due to limited space, only basil, sage, rocket and thyme were grown under plastic film, and no white plastic control cover was included for the same reason. The plants were placed on trolleys (1.5 m × 2 m) with the plastic film on the top and sides at plant level. To ensure sufficient air flow through the plant canopy and satisfactory climate control, a 5 cm gap was left between the sides and the top cover. The pots were spaced at a density of 16 pots m^{-2} in daylight as well as under the cover. No border plants were used due to limited space.

At the end of the experiment, plant height (five random shoots per pot), number of nodes, leaf area, the fresh and dry weight of the aboveground biomass, were recorded. The dry weight was determined at 60 °C in a forced-air oven.

Six pots (20 seedlings per pot) per treatment were used in the experiment. The experiment was repeated once. Since the plants reached somewhat different sizes in the two experiments relative units (relative to the means in the 24 °C MT treatment) in each experiment were used in the statistical analysis. The lemon balm, cilantro, rosemary and oregano data were analysed using a one-way ANOVA with temperature as the main plot. The data of basil, sage, rocket and thyme were analysed using a two-way ANOVA with temperature as the main plot and plastic cover as the sub-plot. The means were separated by using a Fisher's least significant difference test at $P \leq 0.05$. All statistical analyses were performed using Minitab 16 Statistical Software (Minitab Inc., 2010, State College, PA USA).

Results

Increasing the mean MT from 21.7 to 23.7 °C increased the dry weight of cilantro and oregano by 16–18 %, while raising the temperature to 26.2 °C increased the dry weight of basil (32 %), rocket (14 %) and lemon balm (19 %) (Table 2). Raising the temperature from the

Table 1. Climate conditions (means ± SD) during the experimental period.

|	Max. temperature set points (°C)			
	24	28	32	36
Mean temperature (°C)	19.0 ± 1.7	19.9 ± 2.5	21.1 ± 3.3	22.5 ± 4.4
Mean maximum temperature (°C)	21.7 ± 1.3	23.7 ± 1.8	26.2 ± 2.9	29.1 ± 3.5
Vapour pressure deficit (g m^{-3})	4.1 ± 0.9	4.0 ± 0.6	3.6 ± 0.9	4.0 ± 0.1
CO_2 conc. (µmol mol^{-1})	880 ± 63	903 ± 66	873 ± 62	880 ± 67
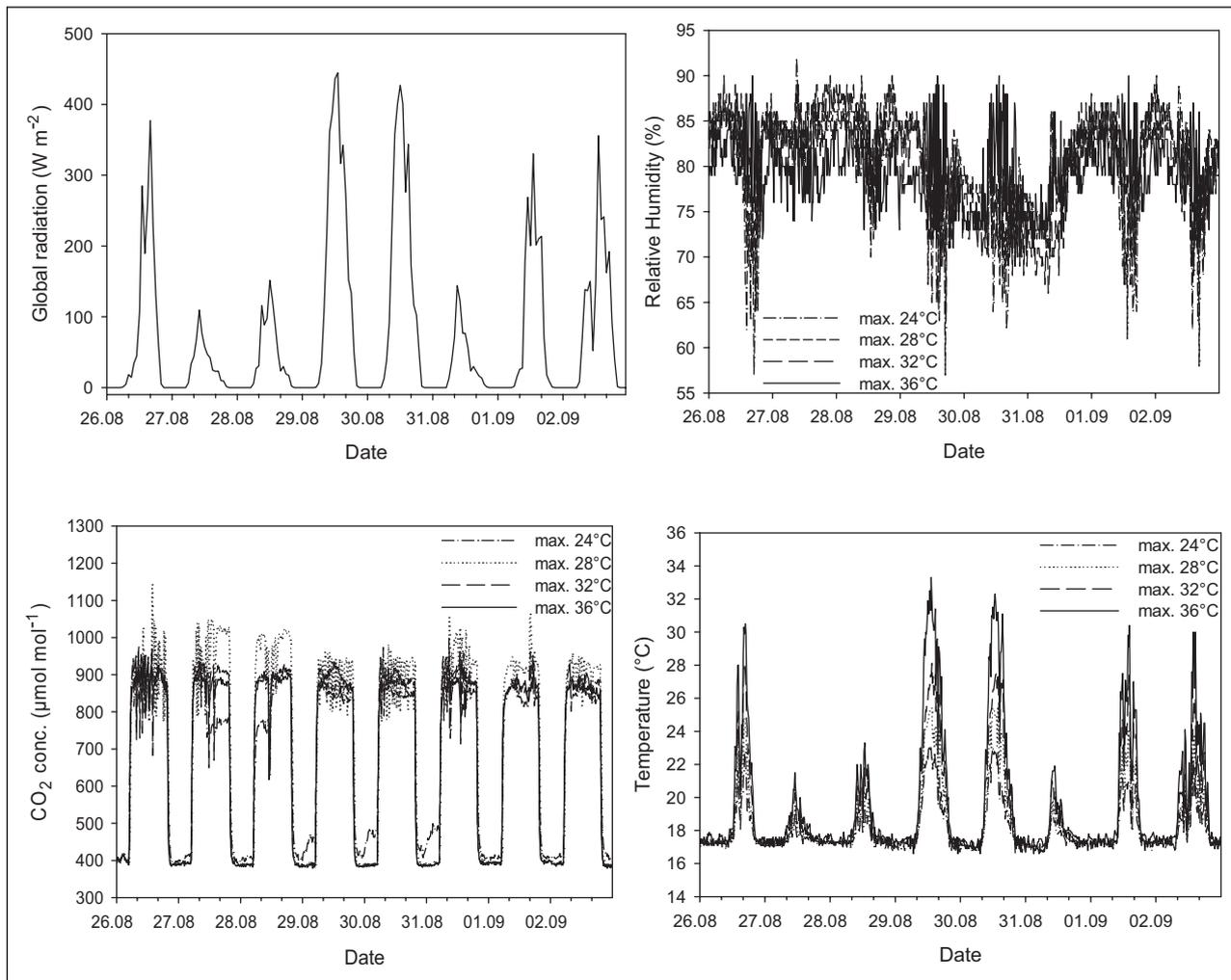
Fig. 1. Global radiation (outside the greenhouse), relative air humidity, CO_2 concentration and temperature as measured in intervals of 15 minutes, during an eight-day period with variable light conditions in the four treatments.

Table 2. Effect of different maximum day temperatures on dry weight and per cent dry weight in parentheses (n = 12, ± SE) of eight herb species grown at 885 µmol mol^{-1} CO_2. Means within each column followed by different letters are significantly different at P ≤ 0.05 level.

Mean max. temperature (°C)	Basil	Sage	Rocket	Thyme	Lemon Balm	Cilantro	Rosemary	Oregano
21.7	2.8 ± 0.1 a (7.0 ± 0.2 a)	4.3 ± 0.3 a (10.2 ± 0.2 a)	3.6 ± 0.5 a (9.7 ± 0.4 a)	3.2 ± 0.2 a (11.8 ± 0.2 a)	5.7 ± 0.7 a (11.8 ± 0.5 a)	5.5 ± 0.4 a (9.3 ± 0.1 a)	1.8 ± 0.2 a (10.4 ± 0.3 a)	3.8 ± 0.4 a (14.2 ± 0.4 a)
23.7	3.4 ± 0.1 b (7.1 ± 0.3 a)	4.5 ± 0.2 ab (10.2 ± 0.2 a)	3.8 ± 0.5 a (10.1 ± 0.5 a)	3.6 ± 0.2 b (12.7 ± 0.4 a)	6.3 ± 0.9 ab (12.6 ± 0.7 a)	6.4 ± 0.6 b (9.1 ± 0.3 a)	2.0 ± 0.2 ab (10.4 ± 0.3 a)	4.5 ± 0.6 b (14.1 ± 0.5 a)
26.2	3.7 ± 0.1 bc (7.2 ± 0.3 a)	4.5 ± 0.2 ab (10.0 ± 0.2 a)	4.1 ± 0.4 b (10.3 ± 0.6 a)	3.8 ± 0.2 bc (12.1 ± 0.3 a)	6.8 ± 0.9 b (12.3 ± 0.7 a)	5.3 ± 0.4 a (9.5 ± 0.2 a)	2.1 ± 0.3 b (10.2 ± 0.3 a)	4.4 ± 0.5 b (14.3 ± 0.5 a)
29.1	3.8 ± 0.2 c (7.4 ± 0.4 a)	4.9 ± 0.3 b (10.4 ± 0.4) a	4.0 ± 0.5 ab (11.7 ± 1.0 b)	4.1 ± 0.1 c (12.0 ± 0.2 a)	6.3 ± 0.8 ab (13.0 ± 0.7 a)	3.9 ± 0.2 c (8.9 ± 0.1 a)	2.2 ± 0.2 b (10.5 ± 0.3 a)	3.9 ± 0.3 ab (14.4 ± 0.7 a)

minimum to the maximum temperature increased the dry weight of sage, thyme and rosemary by 14–22 %. The per cent dry weight of the plants was only slightly affected by the temperature (Table 2). The plant height increased 9 % in cilantro, 14 % in oregano, 20 % in basil, 6 % in rocket, 20 % in lemon balm, 6 % in sage, 0 % in thyme and 22 % in rosemary when the temperature was increased from 21.7 °C to the above-mentioned optimal temperature for dry weight production for the respective species (data not presented). The number of internodes significantly ($p < 0.05$) increased in sage (13 %), rocket (12 %), thyme (13 %), lemon balm (6 %), rosemary (8 %) and oregano (5 %), while was not affected in basil and cilantro (data not presented). Leaf size was not affected by temperature in basil (about 15 cm²), sage (about 14 cm²), rocket (about 12 cm²), cilantro (about 23 cm²), rosemary (about 3 cm²) or oregano (about 5 cm²), while leaf size significantly increased from 15.5 to 17.7 cm² ($P < 0.05$) in lemon balm when the maximum temperature increased from 21.7 to 26.2 °C (data not presented).

The application of coloured plastic film reduced the dry weight of basil by 29 %, sage by 33 %, rocket by 28 % and thyme by 46 % (Table 3). The per cent dry weight significantly decreased when the cover was applied. This means that the plastic film had significantly less effect on the fresh weight of the four species (0–32 %) than the dry biomass (data not shown). Plant height was slightly reduced by the plastic film in basil, sage and thyme, while it was slightly reduced at the lowest temperatures and slightly increased at the highest temperatures in rocket (Table 3). The application of the plastic film resulted in a significant increase ($P < 0.05$) in leaf size in basil (15 %), a decrease in sage (16 %), while it did not affect rocket (Table 3).

Discussion

The relatively small effect on dry weight (14–32 %) achieved by increasing the mean maximum temperature above 21.7 °C might be attributed to the relatively moderate effect on mean day temperature (increased from 19.0 to maximum 22.5 °C). The relatively small increase in the mean temperature was due to relatively few days of high solar radiation during the experimental period. Previously, it has been found that the fresh weight of basil was significantly higher at 30/12 °C (mean temperature 24 °C) compared with 24/12 °C day/night temperature (mean temperature 20 °C) when the photoperiod was 16 h (Putievsky 1983). In the same experiment, however, the lower temperature was more beneficial for oregano. The present experiment also shows that basil responds better to higher temperatures than oregano. Fraszczak and Knaflewski (2009) found that the fresh weight was higher at 15/10 °C than at 20/15 °C day/night temperature. Because of the very low light level (2.9–3.8 mol

Table 3. Effect of daylight, with (DL + cover) and without plastic film cover (DL), on growth (n = 48, ± SE) of four herb species grown at 885 µmol mol⁻¹ CO_2. Significance levels: ns, $P > 0.05$; *, $P \leq 0.05$; **, $P \leq 0.01$; ***, $P \leq 0.001$.

Light treatment	Basil				Sage				Rocket				Thyme		
	Dry w. (g)	% dry w.	Height (cm)	Leaf size (cm²)	Dry w. (g)	% dry w.	Height (cm)	Leaf size (cm²)	Dry w. (g)	% dry w.	Height (cm)	Leaf size (cm²)	Dry w. (g)	% dry w.	Height (cm)
DL	3.4 ± 0.1	7.1 ± 0.2	16.0 ± 0.3	11.0 ± 0.3	4.6 ± 0.1	10.2 ± 0.1	17.1 ± 0.3	12.1 ± 0.4	3.9 ± 0.2	10.4 ± 0.3	12.4 ± 0.4	9.3 ± 0.6	3.7 ± 0.1	12.1 ± 0.2	12.5 ± 0.1
DL + cover	2.4 ± 0.1	5.6 ± 0.1	15.2 ± 0.4	12.9 ± 0.4	3.2 ± 0.1	7.9 ± 0.1	15.3 ± 0.3	10.9 ± 0.3	2.8 ± 0.1	6.6 ± 0.1	12.9 ± 0.3	10.9 ± 0.5	2.0 ± 0.1	9.6 ± 0.1	11.3 ± 0.1
Significance level:															
Light	***	***	*	***	***	***	***	**	***	***	*	***	***	***	***
Light × temp.	ns	ns	ns	ns	ns	ns	ns	ns	ns	**	ns	ns	ns	ns	ns

m^{-2} d^{-1} PAR or 66 µmol m^{-2} s^{-1} PFD) during a photoperiod of 16 h, however, the optimal temperature for growth is expected to be low. Beaman et al. (2009) studied the growth of basil at 100, 400, 500 and 600 µmol m^{-2} s^{-1} PFD and found that 500 µmol m^{-2} s^{-1} PFD was optimal for growth. However, with a temperature control of 25 ± 4 °C, the effect of the high PAR (28.8 m^{-2} d^{-1}) was probably related to a higher temperature at the higher PFD levels. The dry weight of relatively light-demanding pot plants such as pot roses, are expected to be light saturated at about 10–12 mol m^{-2} d^{-1} PAR when grown under artificial light (Mortensen 2004). In daylight, however, the optimal PAR will probably be somewhat higher since the plants cannot efficiently utilise the highest PFD levels of the daylight. Indeed, Chang et al. (2008) found that the dry weight of basil was the same when grown at 13.5 and 24.9 mol m^{-2} d^{-1} PAR. Care should generally be taken when high irradiance levels are applied since this will often strongly increase the temperature of the micro-climate around the plant as well as plant temperature. Lasseigne et al. (2007) cultivated sage at the very high PAR of 34.7 mol m^{-2} d^{-1} in artificial light, and found the top dry weight often increased in temperatures up to 25–30 °C. Previous results in growth chambers with a PFD level of 160 µmol m^{-2} s^{-1} given 16 hours per day (9.4 mol m^{-2} d^{-1} PAR) showed an increase in fresh weight of 20–61 % in the same eight species as used in the present experiment when the temperature was increased from 21 to 24 °C (Mortensen 2004, unpublished results). In this experiment, when the plants were grown at a constant temperature of 18, 21, 24 and 27 °C, the maximum weight was generally reached at 24–27 °C. Decreasing the temperature from 27 to 15 °C during 12 hours per day significantly decreased the weight in all species except cilantro, thyme and oregano.

Using the coloured plastic film was found to considerably increase the red/far red ratio of the daylight thus resulting in a significant reduction in dry weights. This could be attributed to the reduction in PAR by the cover. As expected, the increase in red/far red generally caused a shoot reduction (Rajapakse and Kelly 1992; Patil et al. 2001; Stapel et al. 2011). This was the case even when the PAR level was 34 % lower, a reduction in light (without change in red/far red ratio) that probably would have increased the height. However, the reduction in shoot elongation as a result of using the film was less than the reduction in dry weight, which indicates a less robust plant and reduced plant quality.

It can be concluded from the above discussion that temperatures up to at least 25 °C mean maximum temperature will have a positive effect on the growth of many herbs. If the PAR level at plant level is above around 12 mol m^{-2} d^{-1}, it is unlikely that such high temperatures will have any negative effect on plant quality (shoot elongation). This will be the case, in particular, if the plants are grown at high CO_2 concentrations that are likely to increase the optimum temperature for growth (Mortensen

and Gislerød 2012). Growth at high CO_2 concentrations will also protect the plants against high-temperature damage (Taub et al. 2000). Chang et al. (2005) also found that the volatile oil content strongly increased when basil was grown at 25–30 °C instead of 15 °C. Therefore, the taste of the herbs might also be affected by the temperature, however, this was not recorded in the present study.

Acknowledgements

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Addresses of authors: A.B. Hückstädt, L.M. Mortensen (corresponding author), H.R. Gislerød, Department of Plant and Environmental Sciences, the Norwegian University of Life Sciences, P.O. Box 5003, 1432 Ås, Norway, e-mail (corresponding author): lei-mo@online.no.

Paper II

The Effect of Maximum Day Temperature on Growth and Yield of Tomatoes grown at high CO_2 level

A.B. Hückstädt, L.M. Mortensen, and H.R. Gislerød

The Norwegian University of Life Sciences, Department of Plant and Environmental Sciences, P.O. Box 5003, NO-1432 Ås, Norway

Summary

The effect of maximum day temperatures (MT) of 24, 28, 32 and 36°C on plant growth and fruit production was studied in three tomato cultivars at a daytime concentration of 870 µmol mol^{-1} CO_2, irrespective of irradiance level, from May to September. At the end of June, the plants exposed to a MT of 36°C were so severely injured with no fruit development that this treatment was stopped. The total yield of fruits >45 mm in diameter over the entire period was highest at 24°C MT (mean MT of 23.3°C) amounting to 44.5 kg m^{-2}, while the yield at 28°C MT (mean MT of 26.3°C) was reduced by 18% and by 46% at 32°C MT (mean MT of 29.3°C). The percentage fruit dry weight increased with increasing MT. The number and weight of small fruits (<45 mm) increased strongly with increasing MT. The total dry weight, including fruits and vegetative parts of the plants, was similar at 24, 28 and 32°C MT. The dry weight allocated to the fruits >45 mm (saleable fruits) was 56, 49 and 36% of the total plant dry weight (fruits included) in the 24, 28 and 32°C MT treatment, respectively. The reduction in fruit yield at increased MT was probably due to poor pollination. It was concluded that even in a very accurately controlled high CO_2 environment, the maximum temperature should not exceed 24°C. However, it is still an open question whether a lower night temperature combined with the high day temperature would change this conclusion.

Key words: Daylight – growth – high CO_2 concentration – temperature – tomato – yield

Introduction

It is well known that CO_2 enrichment up to 800-1000 µmol mol^{-1} improves growth and yield of tomato (YELLE et al. 1990). However, during the periods of the day when the irradiance level is highest, ventilation occurs and there is a drop in the CO_2 concentration and photosynthesis. In a closed greenhouse with active cooling, however, ventilation is avoided and a high concentration can therefore be maintained (QIAN et al. 2011). In light-demanding crops such as cut roses, where the photosynthetic rate increases up to about 1000 µmol m^{-2} s^{-1} photon flux density (JIAO et al. 1988), a 50% increase in photosynthesis can be achieved by maintaining a high CO_2 concentration during the high-light periods in the middle of the day at about 32°C (MORTENSEN and GISLERØD 2012b). The potential increase in light use efficiency converting solar energy into biomass, is therefore substantial if the greenhouse can be kept closed during the day. However, the installation cost of the cooling devices and the energy needed to cool the greenhouse are the main obstacles. If a high concentration is to be maintained during periods when the vents are wide open, huge amounts of CO_2 gas is needed (QIAN et al. 2011) which usually is very expensive. Increasing the acceptable temperature in the greenhouse will reduce these costs by reducing the cooling capacity or by reducing the need for ventilation. It is known that CO_2 enrichment of the greenhouse atmosphere and higher irradiance levels increase the optimal temperature for photosynthesis (BERRY and BJÖRKMAN 1980b). At a high CO_2 concentration (800 µmol mol^{-1}) under high-light conditions, the photosynthesis of cucumber plants was found to be the same at 35°C and 25°C (MORTENSEN and GISLERØD 2012). This raises the question of whether a higher maximum temperature than that usually recommended is acceptable if a high CO_2 concentration can be maintained at high irradiance levels. Tomato is a crop that is strongly affected by temperature in terms of crop growth and yield. The optimal temperature for plant growth is normally in the range 18 to 25°C, and for flowering 17°C to 27°C (HEUVELINK 2005). Our aim in the present study was to evaluate the effect on growth and yield of increasing the maximum temperature in intervals of 4°C from 24 to 36°C in an environment where the CO_2 concentration was maintained at a constant high level during the light period. The higher the acceptable maximum temperature (without loss of yield and quality), the lower it will cost to maintain a high CO_2 concentration.

Material and Methods

Seeds of tomato (*Solanum lycopersicum* L.) cvs. Capricia, Cederico and Mecano were sown in 12-cm pots with peat (Veksttorv, Ullensaker Almenning, Nordkisa). The pots were covered with white plastic until germination. The temperature was set to 22/20°C day/night,

and supplemental light was applied to the seedlings at a photon flux density (PFD) of 100 μmol m^{-2} s^{-1} when the outside global radiation fell below 100 W m^{-2} (225 μmol m^{-2} s^{-1} PFD). The photoperiod was 14 hours. When the plants developed the first inflorescence, they were potted in black 30-litre pots in a peat/perlite mixture of 70/30%, and transferred to the experimental conditions. The experiment was carried out in the Phytotron at the Centre for Plant Research in Controlled Climate (SKP) in Ås, Norway (59° 40' N; 10° 46' E) in daylight only. Six plants of each cultivar were placed in one of four phytotron compartments at a density of 4.7 plants per m^{-2}. The pots were wrapped in white plastic foil to prevent them being direct heated by the sunlight. The night temperature was 15.3°C±0.3, while the day temperature was controlled in relation to the solar radiation. With every 100 W m^{-2} increase in global radiation, the air temperature was allowed to increase by 1.8, 2.6, 3.4 and 4.2°C to maximum temperatures (MT) of 24, 28, 32 and 36°C in the four compartments, respectively (Fig. 1). The MT was reached at 500 W m^{-2} global radiation (1125 μmol m^{-2} s^{-1} PFD). The time delay in the temperature control system was ten minutes in order to prevent rapid changes due to variable cloud cover. The day length varied from 19h in June to 12h in September. The mean outside PAR during the experiment was 34.9 mol m^{-2} day^{-1}, and the greenhouse cover transmission was 50%. The experiment was conducted from 21 April until 3 October. At the end of June, the plants exposed to 36°C MT were severely injured and had developed no fruits and were therefore excluded from the remainder of the experiment. The mean MT during the experimental period was 23.4, 26.5 and 29.6°C, while the mean temperature was 17.6, 18.6 and 20.1°C under the 24, 28 and 32°C MT treatments, respectively (Table 1). The mean relative humidity (RH) was about 85%.The mean vapour pressure deficit (vpd) during the day and night period is given in Table 1. The CO_2 concentration in the compartments was 867±85 μmol mol^{-1} during the light period, and about 400 μmol mol^{-1} (outside level) during the night period. The pots were watered twice a day with a nutrient solution (60% Superba Red and 40% Calcinit, Yara, Norway) until complete saturation of the substrate. The conductivity in the pots was maintained at 8.0 mS cm^{-1} and the pH at 5.5.

The pollination of the plants was carried out manually by shaking the plants daily. Axillary shoots and the lower leaves were removed (leaving 15-17 leaves on the plant) once a week, and the fresh and dry weight were determined. There was no regulation of the number of flowers per truss.

The harvesting of the fruits started on 30 June and ended on 3 October. Whole trusses were harvested when the last fruit on the truss changed colour from orange to red. The weight of

the complete truss including the stem was recorded. The fruits were then divided according to whether they were larger or smaller than 45 mm using a calliper, and the number in each group was recorded. Random fruits that were smaller than 45 mm were cut to see whether they were seeded. The diameter and fresh weight of fruits larger than 45 mm were recorded. Random samples were taken from these fruits to determine the dry weight (seven days in a forced-air oven at 60°C).

At the end of the experiment, the shoot length from soil to apex, the number of internodes as well as the fresh and dry weight of the leaves and the stem were recorded.

The data from the fruits, as well as from the plants, were analysed using a one-way ANOVA, with the temperature as the main plot based on the data obtained from the treatments. Cultivars were used as replicates. All statistical analysis was performed using Minitab 16 Statistical Software (Minitab Inc., 2010, State College, PA USA).

Results

The 36°C MT was terminated at the end of June due to serious deformation of the leaves and no normal fruit development. The yield of fruits larger than 45 mm was highest at 24°C MT, and decreased by 18% and 46% at 28 and 32°C MT, respectively (Table 2). This was mainly due to a decrease in the number of fruits, but also partly to a lower fruit weight. Increasing MT from 24°C to 32°C increased the number of small fruits (<45 mm) resulting in a tripling of the fresh weight of the small fruits (including the truss stem). Generally, fruits with a diameter of less than 45 mm were confirmed to be seedless by visual observation when they were cut. The dry weight of the fruits >45mm decreased 14 and 39% when MT was increased from 24°c to 28 and 32°C, respectively (Table 3). The total dry weight of all vegetative parts of the plants removed during and at the end of the experiment and of the harvested fruits, did not differ significantly between the treatments (Table 3). The ratio between dry weight of the fruits >45 mm and total plant dry weight (fruits included) therefore was significantly decreased with increasing MT. Shoot length and the number of leaves were not significantly affected by MT while internode length decreased by 9% when MT increased from 24 to 32°C.

Discussion

Using a MT of 36°C caused deformation of the leaves and was clearly too high for normal plant and fruit development in a high CO_2 environment. This was probably caused by an accumulation of starch in the leaves due to the lack of sink (poor fruit development) (HEUVELINK 1989b). However, the total biomass remained largely unaffected by increasing

the MT from 24 to 32°C when a high CO_2 concentration was maintained. This is in line with the results of previous photosynthesis studies on whole plants in roses and cucumber (MORTENSEN and GISLERØD 2012b; MORTENSEN et al. 2012b). It is well known that doubling the CO_2 concentration increases photosynthesis and growth in the magnitude 30-40% (MORTENSEN 1987a). This means that a significantly higher biomass production can be expected at 32°C by not ventilating the greenhouse compared with ventilation at 24°C, which results in a drop in CO_2 concentration. A higher temperature means less cooling capacity is needed in a closed greenhouse or that the volume of CO_2 gas needed to maintain a high concentration is reduced. However, although the total biomass can be maintained at a high MT, the harvested fruit biomass was significantly reduced by increasing the MT above 24°C. This was due to a reduction in the number and size of the fruits. From previous studies the harvest index (dry weight of the fruits to the total plant dry weight) has been found to be in the range 54-60% (HEUVELINK 1995). While the present result at the 24°C MT treatment is within this range, the 32°C MT treatment gave much lower value. The yield of 44.5 kg m^{-2} from June to September at 24°C MT was high compared to a typical yield of about 50 kg m^{-2} for a whole season (DE GELDER et al. 2005). Very high photosynthetic rates at the high CO_2 concentration during periods of high PAR probably contributed to this high yield (MORTENSEN et al. 2012b).

A high MT resulted in small and seedless fruits in agreement with the known effect of high temperatures (32/26°C day/night temperature) in tomato (SATO et al. 2001). ADAMS et al. (2001) concluded that a high temperature during fruit development as well as during pollination stimulates the development of partly parthenocarpic fruits. KHANAL et al. (2013a), however, found a higher number of pollen as well as better germination in the present tomato cultivars when the plants were grown under 32/11°C compared to a 24/17°C day/night temperature. In this case, the mean temperature was kept constant, which indicates that the reduced pollen production and germination is related to the increased mean temperatures. In the present experiment, the mean temperature increased from 17.6°C to 20.1°C when MT increased from 24 to 32°C. The reduction in fruit size was probably more due to an increase in the mean temperature than to an increase in MT. Compensating for the high maximum day temperature by decreasing the night temperature may have improved fruit development and size. However, the manual shaking of the trusses was also probably inadequate for efficient pollination (MORANDIN et al. 2001). The reduction in fruit development at high MT did not reduce the total biomass production in the present experiment in accordance with the

conclusion reached by HEUVELINK AND BUISKOOL (1995) i.e. that production does not depend on the sink-source ratio.

It might be concluded that increasing the maximum day temperature above 24°C will decrease the tomato yield even if a high CO_2 level is maintained irrespective of irradiance level. However, the question is still open whether a lower night temperature can compensate for the high day temperature to secure good pollination and fruit development.

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Figure1. Photosynthetic active radiation (PAR) outside the greenhouse, daily mean temperature and daily maximum temperature in the four temperature treatments during the experimental period. The treatment with a maximum temperature of 36°C was stopped at the end of June.

Figure 2. Cumulative yield of the whole truss and of fruits >45 mm only, at three different maximum temperature treatments (n=3, ±SE) during the harvesting period from July to October.

Table 1 Mean day and night temperature, mean day maximum temperature, relative humidity (RH) including day and night, and vapour pressure deficit (VPD) for the day and night period separately, for three different maximum temperature (MT) treatments. All values are means ± SD.

	Temperature (°C)				RH (%)	VPD (g m^{-3})	
MT treatments	Mean	Day period	Night period	Mean day max.	Day and night	Day	Night
24°C	17.6±3.3	18.9±3.4	15.1±0.5	23.4±2.2	85±6	2.7±0.5	1.8±0.6
28°C	18.6±4.6	20.4±4.7	15.1±0.7	26.5±3.4	88±4	2.9±0.7	1.5±0.7
32°C	20.1±5.7	22.1±5.9	15.7±0.9	29.6±4.3	83±4	3.9±0.2	2.7±0.9

Table 2. The yield (fresh weights) and characteristics of fruits >45 mm and yield of fruits <45 mm (including truss stem) as a mean of three tomato cultivars (n=3, ±SE) grown at three maximum temperature levels (MT). Significance levels: ns, p>0.05; *, p≤0.05; **, p≤0.01; ***, p≤0.001.

	Fruits >45 mm						Fruits < 45 mm	
MT (°C)	Yield (kg m^{-2})	No of fruits (m^{-2})	No of trusses harvested (m^{-2})	Mean fruit diameter (mm)	Mean fruit fresh weight (g)	% fruit dry weight	Yield (kg m^{-2})	Total fresh w. (kg m^{-2})
24	44.5±3.2	414±25	51.3±0.7	61.1±0.2	107.2±0.9	6.1±0.04	4.0±0.5	48.5±2.7
28	36.3±3.3	357±13	51.0±1.5	59.5±0.2	101.9±1.1	6.4±0.04	6.7±0.8	43.0±2.6
32	24.0±1.4	286±5	57.6±2.6	55.7±0.2	85.1±1.1	6.8±0.05	12.5±1.3	36.5±1.1
Sign. level:								
Temp.	**	**	ns	***	***	***	**	*

Table 3. Growth variables as measured at the end of the experiment as means of three tomato cultivars (n = 3, ±SE) grown at three maximal temperature levels (MT).

| MT (°C) | Shoot length (cm) | No of leaves per stem | Internode length (cm) | Dry weight (g m^{-2}) | | Ratio fruit w. >45 mm/total weight |
				Fruits > 45 mm	Total plant dry weight	
24	337±10	51.5±1.2	6.5±0.1	2655±136	4765±107	0.56±0.02
28	324±9	52.4±1.4	6.2±0.1	2319±181	4756±88	0.49±0.04
32	312±5	53.3±0.7	5.9±0.1	1649±137	4619±102	0.36±0.03
	ns	ns	***	**	ns	**

Fig. 1
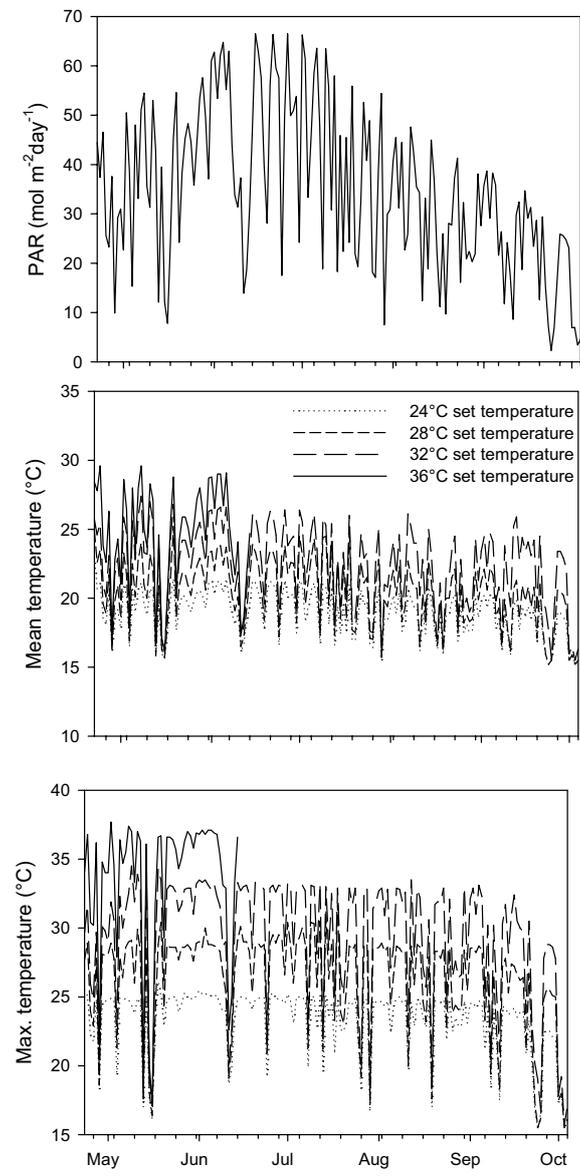
Fig. 2
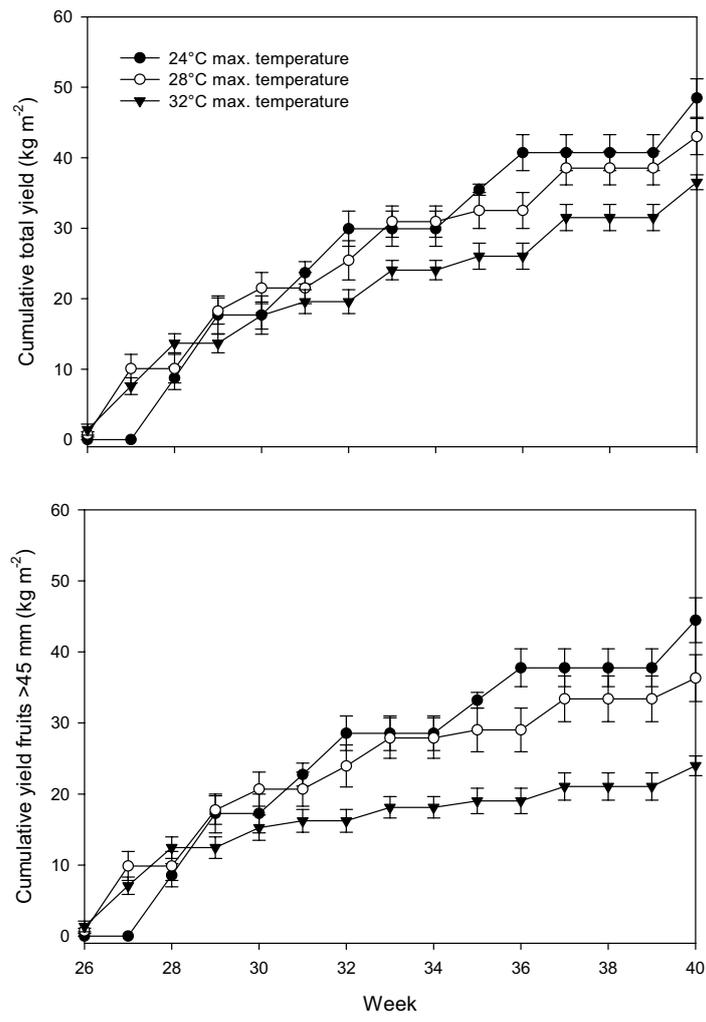
Paper III

❖❖ Scientific
❖❖ Research

The Effect of High Day and Low Night Temperature on Pollen Production, Pollen Germination and Postharvest Quality of Tomatoes

B. Khanal, A. Suthaparan, A. B. Hückstädt, A. B. Wold, Leiv Mortensen, H. R. Gislerød

Department of Plant and Environmental Sciences, The Norwegian University of Life Sciences, Ås, Norway.
Email: lei-mo@online.no

ABSTRACT

Temperature integration where high day temperatures are compensated by lower night temperatures is one strategy that can be used to reduce energy consumption in greenhouses. Crop tolerance to temperature variation is a prerequisite for using such a strategy. Greenhouse experiments were conducted on tomatoes cvs, Capricia, Mecano and Cederico in order to investigate the effect of different day/night temperature regimes (24/17, 27/14 and 30/11°C) where the same mean temperature was maintained for the production and germination of pollen. In addition, fruit quality as determined by fruit firmness, dry matter content, soluble solids, titratable acids, and pH was examined at harvest and after seven and 14 days of storage. The 30/11°C treatment significantly increased pollen production and germination compared to the 24/17°C treatment, while the 27/14°C treatment was generally in between the other two treatments. Fruits grown at the 27/14°C treatment were significantly firmer, while fruits grown at 24/17°C had higher dry matter content, soluble solids, and titratable acids compared to the other treatments. There were significant differences between cultivars with respect to firmness, dry matter, titratable acidity, and pH. The quality of the fruits changed during storage, but the storability of the tomatoes was not affected by preharvest temperature treatments. The overall conclusion was that the 27/14°C treatment was superior to the other two temperature treatments with respect to the studied parameters.

Keywords: Daily Mean Temperature; Day Temperature (DT); Night Temperature (NT); Pollen; Temperature Integration; Dry Matter; pH; Titratable Acids; Soluble Solids; Postharvest; Tomato

1. Introduction

Temperature integration where high day temperatures are compensated by lower night temperatures is an important means of reducing energy consumption in greenhouses [1]. Temperature increases with increasing irradiance to a maximum accepted level at which ventilation takes place, and the night temperature is reduced sufficiently to secure an optimal mean temperature level. Depending on the season and weather conditions, energy savings of more than 20% can be achieved by means of such temperature control [2,3]. However, the effectiveness of temperature integration depends on the plant's ability to tolerate temperature variation. Results of studies conducted on a wide range of vegetables including tomato and ornamentals, have shown that within a certain temperature range, growth and development respond to the mean daily temperature rather than to the day/night temperature variation [4-6].

Tomato is an important vegetable worldwide, in which temperature is known to affect various physiological aspects, including pollen viability and fruit quality [7]. It has been reported that pollen germination was significantly reduced when tomatoes were grown at temperatures of up to 32/26°C day/night temperature [8]. Tomato quality includes visual characteristics such as color and firmness, nutritional constituents, and organoleptic characteristics such as aroma compounds and the content of sugar and acids. Dorais *et al*. (2001) reviewed the quality of greenhouse tomatoes [9], and the fruit quality might be affected by high and low temperatures as well as the differences between day and night temperatures [10]. The effect of preharvest and postharvest factors, including temperature, on soluble solids in tomatoes has been reviewed [11]. For cherry tomatoes, the percentage dry weight, glucose, and fructose were found to be higher in fruits developed under high temperature variation (30/

15˚C day/night), while lower levels of citric and malic acid were reported [12]. Nevertheless, few works have included the effect of preharvest factors on the quality and storability of tomatoes [13]. It has been concluded that tomato plants can tolerate air temperature fluctuations of up to 6˚C from the daily mean of 18.7˚C with respect to growth and flowering [14]. Little is known about the effect of temperature variation, with a fixed daily mean temperature, on pollen growth, fruit quality, and storability. The aim of this study was therefore to examine the effect of different day/night temperature variations on pollen production and germination as well as on the postharvest fruit quality of three tomato cultivars.

2. Materials and Methods

2.1. Plant Material and Environmental Conditions

Seeds of tomato (*Solanum lycopersicum* "Capricia", "Mecano" and "Cederico") were sown in 12-cm plastic pots filled with peat (VEKSTTORV, Ullensaker Almenning, Nordkisa, Norway) and perlite (Substraat, RHD, The Netherlands) mixture (3:1). Plants were irrigated with a complete nutrient solution (Superba^{TM} Red (50%) and Calcinite (50%), Yara AS, Oslo, Norway) as necessary. Temperature (day and night) and relative air humidity (RH) were set to 20˚C (a mean of 19.7˚C observed) and 75% (a mean of 72% observed). Supplemental lighting at a photon flux density (PFD) of 100 µmol m^{-2}·s^{-1} was provided by high-pressure sodium lamps (HPS) (Lucalox LU400/XO/T/40, GE lighting, Budapest, Hungary) when the outside level fell below 100 W·m^{-2} global radiation, to maintain 20-hour day length. The PFD was measured by a quantum meter Model QMSW-SS (Apogee instruments Inc., Logan, UT, USA). Once the tomato plants had developed five leaves, they were transplanted into 30-liter plastic pots filled with a peat and perlite mixture (7:3). At the appearance of the first inflorescence, the plants were moved to the experimental conditions.

The experiment was conducted at the Norwegian University of Life Sciences (UMB), Ås, Norway (59˚ 40'N and 10˚ 46'E) from March to July 2011, in three greenhouse compartments located beside each other. The ventilation temperature for the different compartments was 24˚C, 27˚C, and 30˚C during the day, and ventilation was used at night to reach temperatures of 17˚C, 14˚C, and 11˚C, respectively. Solar radiation, air temperature, and RH in the greenhouse compartments were recorded at five-minute intervals by a Priva greenhouse computer (Priva, Zijlweg, The Netherlands). The hourly mean values (mean of 12 readings) of these variables were used to calculate the mean day, night, and daily temperatures.

During the experimental period, the mean day temperatures in the three compartments were 23.7˚C ± 1.8˚C, 26.4˚C ± 1.3˚C, and 29.2˚C ± 2.0˚C, and the mean night temperatures were 16.4˚C ± 0.1˚C, 13.9˚C ± 0.1˚C, and 11.5˚C ± 0.5˚C, respectively. The temperature, air humidity, and CO_2 concentration were measured at plant level. During the experimental period, the day length varied from 11 hours in March to 19 hours in June, and no supplementary lighting was used. At sunrise, the vents were closed and the temperature was allowed to increase by means of solar radiation. Night temperatures were achieved by natural cooling through ventilation or by heating. The air humidity was maintained at 75% ± 5% day and night through ventilation or by the application of mist. The CO_2 concentration (as measured every ten minutes) by a Priva infrared gas analyzer) was set to 700 µmol·mol^{-1} during the light period when the vents were closed, and to 385 µmol·mol^{-1} during ventilation or during the dark period. The mean concentration for the whole experimental period was 628 ± 82, 662 ± 77, and 715 ± 76 µmol·mol^{-1} at the 24/17˚C, 27/14˚C, and 30/11˚C treatments, respectively. The temperature and CO_2 concentration during a period of six or 12 days at the time of flowering are summarized (**Table 1**) as well as the temperature during the four weeks prior to harvest (**Table 2**). The photosynthetic active radiation (PAR) inside the greenhouse (about 50% of the outside radiation) during the 12 days was 13.3 ± 3.1 (17 - 28 March) and 12.2 ± 6.4 mol m^{-2}·day^{-1} (29 March-10 April) for truss number four and six, respectively. The photosynthetic active radiation was 17 ± 6, 20 ± 6 and 20 ± 10 mol·m^{-2}·day^{-1} in April, May and June, respectively. The conversion factor from global radiation (in MJ·m^{-2}·day^{-1}) to PAR (in mol·m^{-2}·day^{-1}) was 2.2.

Elemental sulfur was applied for two hours every night. Plants were fertilized daily with four liters (complete saturation of the substrate) of the same nutrient solution as previously described. The nutrient solution had a conductivity of 2.5 mS·cm^{-1} (DGT Volmatic Type LM20 Serial 9305), and the salinity of the growing medium was 4 - 5 mS·cm^{-1}, using the soil saturated extract (SSE) method.

The plants were pinched above the ninth truss in all temperature treatments. The fourth and sixth trusses as counted from the bottom of the plants were selected for the following analysis: The first flower was assessed for pollen production and the second flower for pollen germination one day after opening, and the third flower for pollen production and the fourth flower for pollen germination four days after opening. This was done under the same conditions (20˚C/70% RH) for all three temperature treatments. In addition, the fifth and sixth flowers on the same trusses were used to assess pollen pro-

Table 1. Day and night temperature (means ± SD) during a six-day period (from five days before until one day after flower opening) or a twelve-day period (from eight days before until four days after flower opening) in trusses four and six. CO_2 concentration is given for the light period.

Set temperature (˚C)	Truss no.	Day temp. (˚C)		Night temp. (˚C)		Mean temp. (˚C)		CO_2 conc. (μmol·mol^{-1})
		6-day period	12-day period	6- day period	12-day period	6- day period	12-day period	6-day/12-day period
24/17	4	23.7 ± 1.3	23.9 ± 1.2	16.4 ± 0.1	16.3 ± 0.1	19.1	19.2	632 ± 82/618 ± 80
27/14	4	26.0 ± 1.1	26.4 ± 1.4	13.9 ± 0.1	13.8 ± 0.1	18.2	18.4	630 ± 76/652 ± 91
30/11	4	28.7 ± 2.3	29.1 ± 2.2	11.4 ± 0.2	11.1 ± 0.2	17.5	17.7	652 ± 88/716 ± 94
24/17	6	22.3 ± 2.1	23.5 ± 2.3	16.5 ± 0.1	16.6 ± 0.1	18.9	19.3	624 ± 82/580 ± 82
27/14	6	26.2 ± 2.4	26.4 ± 2.1	13.9 ± 0.1	14.1 ± 0.1	18.4	18.9	694 ± 78/624 ± 95
30/11	6	29.5 ± 2.3	29.3 ± 2.2	11.1 ± 0.2	12.0 ± 0.7	18.1	18.5	778 ± 73/720 ± 92

Table 2. Mean maximum day and minimum night temperature during the four weeks prior to harvesting the tomato fruits of truss number five for three different temperature treatments.

Set day/night temperature (˚C)	Observed day temperature (˚C)	Observed night temperature (˚C)	Mean temperature (˚C)
24/17˚C	25.4 ± 2.2	15.3 ± 1.4	19.7
27/14˚C	27.2 ± 1.3	14.1 ± 0.5	19.4
30/11˚C	30.1 ± 2.5	11.3 ± 0.5	19.6

duction and germination at their respective growth temperatures. Since the solar radiation is quite variable during spring two different trusses were selected in order to cover a longer time period for climate exposure.

2.2. Pollen Production

In order to measure pollen production, the flowers were removed and placed in 50 ml centrifuge tubes that were filled with 5 ml of distilled water containing 20 μl·l^{-1} of Tween 20 surfactant (Sigma-Aldrich Chemie GmbH, Steinheim, Germany) (one flower per tube). Tubes were shaken by hand 40 times and the flower was removed. The number of pollen per ml of suspension was calculated in two aliquots of suspension using haemocytometer (HYCOR, Hycor biomedical inc. California, USA) under a light microscope at 100X. Pollen with a diameter of less than 20 μm and shrunken pollen were considered undersized or abnormal.

2.3. Pollen Germination

For pollen germination, the flowers were picked with their pedicle and held 2 cm above Petri dishes (5 cm in diameter) containing pollen growth media [15]. Flowers were vibrated for five seconds using an electric tooth brush (Philips HX1610 Double cleaning action, China)

placed on the flower pedicle. Petri dishes were then sealed and incubated in a growth chamber at 20˚C and 70% RH. The day length was 14 hours and 130 ± 10 μmol·m^{-2}·s^{-1} PFD was supplied by high-pressure mercury lamps (Powerstar HQI-BT 400 W/D day light, OSRAM GmbH, Augsburg, Germany). One day after incubation, a piece of the pollen growth media was cut and placed on a microscopic glass slide. A droplet of water was placed on top and covered with cover slips. The samples were then assessed for pollen germination under a light microscope. Pollen containing germ tubes at least half the length of the diameter of the pollen was deemed to have germinated. The first 100 pollens were assessed and the percentage of pollen germination was calculated.

2.4. Fruit Harvest and Postharvest Quality

Forty-five tomato fruits from the third and fifth clusters of each cultivar and temperature treatment were harvested at commercial ripening stage based on comparison with color chart scale 6 - 9 (Ctifl, Code Couleur Tomate, France). At harvest (day 0), 15 tomatoes were randomly selected and divided into three replicates each containing five tomatoes. The color and firmness of the fruits were measured using color chart comparison and DUROFEL DFT 100 digital firmness tester (Agro-Technologie, St Etienne du Gres, France), respectively. For firmness measurements, the tip of the digital firmness tester was placed on the surface of each tomato fruit at three different points. The instrument measured the elasticity of the outer fruit flesh within the range from 0 (no resistance or high elasticity) to 100 (high resistance or no elasticity) and firmness is specified as DUROFEL-units. The remaining 30 fruits were stored in darkness at 13˚C and 85% RH. After seven and 14 days' storage, 15 fruits were assessed for color and firmness. Immediately after the assessments, 3 × 5 fruits were frozen at −20˚C pending further analysis.

2.5. Dry Matter Content, Soluble Solids, Titratable Acidity, and pH

For analysis of dry matter, soluble solids, titratable acidity, and pH, frozen tomatoes were thawed overnight at room temperature. Tomato samples were homogenized using a food processor (BRAUN, Germany). For dry matter assessment, six grams of homogenized material was dried at 104°C for 24 hours and the dry matter percentage was calculated.

The homogenized samples were filtered (125 mm, Whatman GmbH, Dassel, Germany) and the filtrates were used for further analysis. For soluble solids measurement, a digital refractometer, Model Atago Palett PR-100 (Atago Co., Ltd., Tokyo, Japan) was first calibrated using distilled water. Then two to three drops of tomato juice were placed on the sensor of the refractometer. Soluble solids were given as a percentage.

Automatic titrator, Model Methrom 716 DMS Titrino and 730 Sample changer (Metrohm Ltd., Herisau, Switzerland) were used for the measurement of titratable acidity. Ten ml of filtrate was diluted with 50 ml of distilled water. Then sodium hydroxide (0.1N) was added to the diluted filtrate to reach pH of 8.1. Titratable acidity was calculated as a percentage of citric acid. The pH was measured using a pH meter (Model 691 PH Meter, Metrohm Ltd., Herisau, Switzerland).

2.6. Statistical Analysis

Minitab (version 16) was used to conduct analysis of variance (GLM procedure). Three different day/night temperature combinations and three different varieties were included in the model. Response variable means were compared using Tukey's pairwise comparison test at P = 0.05.

3. Results

3.1. Pollen Production (Figure 1)

The number of normal pollen in the fourth truss one day after flower opening was not significantly affected by day/night temperature, while pollen production in the sixth truss was significantly higher (p < 0.05) at 27/14°C and 30/11°C compared to 24/17°C (**Table 3**). The number of normal pollen assessed four days after flower opening as a mean of the three cultivars, increased as DT increased/NT decreased above/below 24/17°C (**Table 3**). The number of abnormal pollen often increased with increasing DT/decreasing NT, particularly in the 30/11°C treatment (**Table 3**). The number of normal pollen was highest in cv. Cederico as measured one day after flower opening in the fourth truss, and in cv. Mecano as meas-
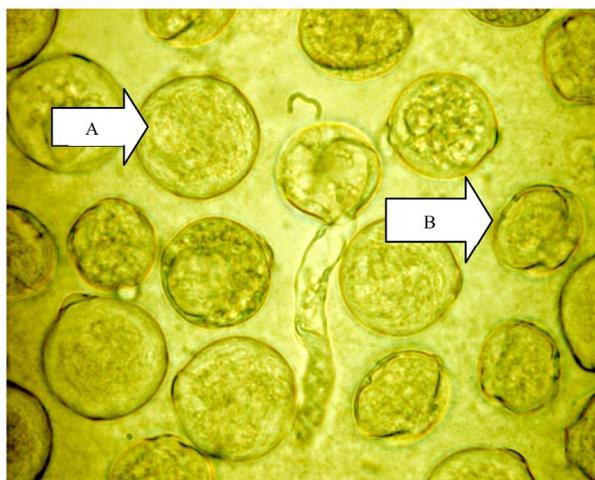

Figure 1. Normal pollen (A) and abnormal pollen (B).

Table 3. Effect of day/night temperature regimes on number of normal and abnormal pollen in different trusses one and four days after flower opening. Values represent means of three cultivars and two replicates (n = 6, ±SD). Different letters within each column indicate significant differences between treatments at p < 0.05 level.

Set temperature (°C)	Truss no.	No. of normal pollen		No. of abnormal pollen	
		1 day	4 days	1 day	4 days
24/17	4	28.1 ± 2.0 a	40.3 ± 2.3 b	8.7 ± 0.8 a	15.0± 1.4b
27/14	4	28.2 ± 2.2 a	41.6 ± 2.3 ab	9.1 ± 1.2 a	18.9±1.5 ab
30/11	4	31.3 ± 2.5 a	48.8 ± 1.6 a	9.3 ± 0.8 a	20.5± 1.3 a
24/17	6	26.4 ± 1.4 b	33.4 ± 1.7 b	11.0 ± 1.2 b	6.7± 0.7 c
27/14	6	45.9 ± 2.9 a	42.1 ± 2.1a	9.3 ± 0.9 b	10.6± 0.6 b
30/11	6	51.0 ± 2.1 a	43.4 ± 1.6a	15.3 ± 1.3 a	15.5± 0.7 a

ured four days after flower opening in the sixth truss (data not presented).

3.2. Pollen Germination

The pollen germination percentage as measured under the same climate conditions (in a growth chamber) generally increased as DT increased/NT decreased (**Table 4**). This was the case in both trusses as well as for pollen harvested one or four days after flower opening (**Table 4**). Similar results were found when pollen germination was measured under growing conditions (**Table 4**). In growth chamber incubation, pollen germination of the cultivar Cederico was significantly higher four days after flower opening in the sixth truss compared to Capricia and Mecano (data not presented).

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3.3. Tomato Quality

Tomatoes grown at 27/14˚C were significantly firmer compared to the other temperature treatments (**Table 5**). Tomatoes grown at 24/17˚C contained significantly higher amounts of dry matter, soluble solids and titratable acidity, whereas pH was higher in tomatoes grown at 30/11˚C. The cultivars Capricia and Mecano had significantly firmer fruits compared to Cederico. No significant differences were found between the cultivars with respect to soluble solids. Significant differences were observed between the cultivars with respect to dry matter, titratable acidity, and pH. Fruit firmness decreased significantly during storage. Dry matter, soluble solids, and pH remained stable during storage, whereas titratable acidity decreased significantly from day seven to day 14. Visually observed the tomatoes produced at 30/11˚C were pale in color compared to tomatoes produced in the other temperature treatments, however, there was no systematic record of the color. The different preharvest temperature treatments had no significant effect on the storability of the tomato fruits (data not shown).

4. Discussion

A climate control strategy where high DT was combined with low NT, a DT of at least about 29˚C combined with a NT of 11˚C - 12˚C, did not have a negative effect on the production and germination of normal pollen. Compared to the control treatment of 24/17˚C, this type of climate was often actually beneficial to pollen production and germination. This was concluded when the pollen was tested under plant growing conditions as well as under the same climate conditions in a growth chamber. Although the number of abnormal pollen under high DT/low NT increased, this was more than compensated by an increased number of normal pollen and increased germination potential. Sato *et al.* (2006) found that increasing the DT to 32˚C combined with a NT of 26˚C had a negative impact on pollen germination in tomato [8]. The maximum DT was higher and the NT much higher than that used in the present experiment. Energy reserves seem to be the predominant factor in determining pollen production as well as pollen viability [16]. Delayed ventilation and higher CO_2 concentration accompanied higher DT, and this probably stimulated the photosynthetic rate. It has been reported that the negative effects of high day temperatures of up to about 30˚C on photosynthesis can be minimized or eliminated by CO_2 enrichment in roses [17,18] and cucumber [19]. Photosynthesis has also been found to be stimulated by higher growth temperatures when the CO_2 concentration was increased [20]. The difference in pollen production in the fourth and sixth truss one day after opening might also be due to longer day lengths.

Table 4. Effect of day/night temperature regimes on percentage pollen germination as measured under the same conditions in a growth chamber and under growing conditions one day and four days after flower opening. Values represent means of three cultivars and two replicates (n = 6, ±SD).

Set temperature (˚C)	Truss no.	Same conditions in growth chamber		At growing conditions	
		1 day	4 days	1 day	4 days
24/17	4	26.4 ± 1.8 b	19.1 ± 1.7 b	15.9 ± 1.7 b	15.1 ± 1.5 c
27/14	4	36.5 ± 2.9 a	24.5 ± 2.2 b	17.0 ± 1.2 b	23.6 ± 1.4 b
30/11	4	41.1 ± 3.5 a	34.8 ± 2.8 a	37.0 ± 2.1 a	37.0 ± 2.1 a
24/17	6	16.2 ± 1.2 c	17.3 ± 1.2 c	18.2 ± 2.1 b	17.1 ± 1.5 c
27/14	6	28.6 ± 2.5 b	25.4 ± 1.6 b	24.4 ± 1.1 b	27.8 ± 1.0 b
30/11	6	40.0 ± 2.0 a	37.7 ± 1.9 a	38.1 ± 2.3 a	41.1 ± 2.2 a

Table 5. Effect of different day/night temperature regimes during growth on firmness, dry matter (%), soluble solids (%), titratable acidity (%) and pH of three tomato cultivars at harvest and after seven and fourteen days of storage (n = 6, ±SD).

Treatments		Firmness	Dry matter (%)	Soluble solids (%)	Titratable acid (%)	pH
Day/Night temperature	24/17˚C	83.6 ± 0.8 b	5.55 ± 0.04 a	5.12 ± 0.04 a	0.450 ± 0.006 a	4.18 ± 0.01 b
	27/14˚C	86.5 ± 0.7 a	4.88 ± 0.05 b	4.64 ± 0.02 b	0.426 ± 0.004 b	4.18 ± 0.01 b
	30/11˚C	81.7 ± 0.8 b	4.89 ± 0.04 b	4.73 ± 0.01 b	0.403 ± 0.003 c	4.23 ± 0.01 a
Cultivars	Capricia	86.5 ± 0.6 a	5.24 ± 0.05 a	4.83 ± 0.05 a	0.438 ± 0.006 a	4.18 ± 0.01 b
	Mecano	84.0 ± 0.5 a	5.11 ± 0.06 ab	4.87 ± 0.04 a	0.422 ± 0.003 ab	4.21 ± 0.00 a
	Cederico	81.2 ± 0.8 b	4.97 ± 0.05 b	4.78 ± 0.03 a	0.418 ± 0.005 b	4.20 ± 0.01 ab
Storage time	0 day	89.1 ± 0.5 a	5.17 ± 0.06 a	4.84 ± 0.04 a	0.427 ± 0.004 ab	4.20 ± 0.01 a
	7 days	84.1 ± 0.5 b	5.14 ± 0.06 a	4.88 ± 0.04 a	0.435 ± 0.006 a	4.19 ± 0.01 a
	14 days	81.7 ± 0.8 c	5.01 ± 0.06 a	4.79 ± 0.04 a	0.417 ± 0.005 b	4.20 ± 0.01 a

Fruits developed at 27/14˚C were firmer than fruits developed under other temperature treatments, and this might be related to the temperature-dependent activity of cell wall degrading enzymes acting on proteins and carbohydrates [21]. The difference in firmness between cultivars could be explained by variation in skin toughness, flesh firmness, and the pericarp/locular material ratio [22]. The firmness decreased during storage, which is most probably related to possible water loss and further ripening of the fruit. This is in accordance with the results of Jha and Matsuoka (2005), where a significant reduction in tomato firmness was observed during storage [23]. The red color of tomato fruit is determined by the amount of lycopene present in pericarp [24,25]. The optimal temperature for lycopene synthesis in tomatoes is in the range 16˚C - 21˚C, and a very high DT (30˚C) in the present experiment reduced the red color as visually observed, even if this high DT was compensated by 11˚C NT.

The dry matter of fruit and vegetables is mainly composed of sugars and acids. Tomatoes usually contain 5% - 8% dry matter of which 4% - 6% is soluble solids [9]. Citric and malic acids are the main organic acids found in tomato fruits and constitute approximately 10% - 13% of the dry matter content [9]. In the present study, the dry matter content of the tomato fruits that could be associated with reduced soluble solids and titratable acids, decreased with increasing DT/decreasing NT. This reflects a somewhat reduced organoleptic quality of the fruits at high DT/low NT. The dry matter and soluble solids content of fruit mainly depends on the synthesis and transport of assimilates from the leaves to the fruits [26]. High temperatures are known to favor the distribution of assimilates to the fruits during fruit development [27], whereas low night temperatures have previously been shown to reduce the content of soluble solids in tomatoes [28]. For cherry tomatoes grown in greenhouses, an increase in sugars and a decrease in titratable acidity were observed in late harvest when the temperature and solar radiation peaked [12]. During storage, the content of soluble solids remained stable whereas the titratable acidity changed significantly. The stability of soluble solids during storage has previously been observed [29,30] and the concentration of titratable acidity has been found to decrease [30] during a seven-day storage period.

5. Conclusion

It can be concluded that significantly larger variations between day and night temperatures than commonly applied will not reduce the pollen production and pollen germination potential in tomato as long as the mean temperature is kept constant. The overall conclusion was that the 27/14˚C treatment was superior to the other two temperature treatments (24/17˚C and 30/11˚C DT/NT). The preharvest temperature regimes did not affect the storability of the tomatoes.

6. Acknowledgements

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Paper IV

The Effect of Low Night and High Day Temperatures on Photosynthesis in Tomato

A.B. Hückstädt, A. Suthaparan, L.M. Mortensen and H.R. Gislerød

Department of Plant and Environmental Sciences, the Norwegian University of Life Science, 1432 Ås, Norway
Email:arne.huckstadt@yahoo.com

ABSTRACT

If low night temperatures can be combined with high day temperatures, providing optimal growth conditions for plants, a significant energy saving can be achieved in greenhouses. Lowering the night temperature from 18°C to 10-11°C for 8 h had no negative effect on the CO_2 exchange rate (CER) during the following light period in tomato. This was found both in plants grown in artificial light only or in combination with daylight. Allowing the temperature to increase from 20°C to about 40°C, in parallel with an increasing solar photon flux density (PFD) from 0 up to about 800μmol m^{-2} s^{-1} in the greenhouse during summer, progressively increased CER when the CO_2 concentration was maintained at 900μmol mol^{-1}. At 400 μmol mol^{-1} CO_2, maximum CER was reached at about 600 μmol m^{-2} s^{-1} PFD combined with a temperature of 32°C, and leveled out with a further increase in PFD and temperature. Maximum CER at high CO_2 concentration was around 100% higher than at low CO_2 level. Under early autumn conditions, CER increased up to about 500 μmol m^{-2} s^{-1} PFD/32°C at low CO_2 and up to about 600 μmol m^{-2} s^{-1} PFD/35°C at high CO_2. An elevated CO_2 level doubled the CER in this experiment as well. Measurements of chlorophyll fluorescence showed no effect of low night temperature, high day temperature or CO_2 concentration on the quantum yield of photosynthesis, indicating that no treatment negatively affected the efficiency of the photosynthetic apparatus. The results showed that low night temperatures may be combined with very high day temperatures without any loss of daily photosynthesis particularly in a CO_2 enriched atmosphere. If this can be combined with normal plant development and no negative effects on the yield, significant energy savings can be achieved in greenhouses.

Keywords: Carbon Exchange Rate (CER); Chlorophyll Fluorescence; CO_2 Concentration; Day Temperature; Night Temperature; Photon Flux Density (PFD); *Solanum lycopersicon* L.

1. Introduction

Within a certain range, plant growth generally depends more on the mean temperature than on the diurnal temperature variation (DE KONING 1988; RIJSDIJK and VOGELEZANG 2000). Temperature integration, where high day temperatures are compensated for by lower night temperatures, has therefore the potential to reduce energy consumption in greenhouses (ADAMS et al. 2011). This implies that the temperature is allowed to increase with increasing irradiance levels up to an acceptable maximum temperature when ventilation takes place. This is done in combination with a drop in night temperature in order to achieve an acceptable mean temperature, a drop that also reduces the heating demand. This means that energy savings of more than 20% can be achieved (SIGRIMIS et al. 2000; KÖRNER et al. 2004). The optimal temperature for photosynthesis is known to increase with increasing irradiance levels as well as carbon dioxide (CO_2) enrichment (BERRY and BJÖRKMAN 1980a; KIM and LIETH 2003). The carbon dioxide exchange rate (CER) in roses was found to increase progressively up to maximum daylight conditions in a greenhouse in summer at elevated CO_2 concentration, despite a temperature increase of up to 32°C (MORTENSEN and GISLERØD 2012a). As it is much easier in practice to maintain a high CO_2 concentration at higher temperatures than at lower temperatures, the high temperatures might be preferred due to higher CER at high CO_2 concentrations. High day temperatures will also heat the greenhouse interior and reduce the heating costs the following night. Most measurements of CER in greenhouse plants have been performed on single leaves, and few studies appear to have been carried out on whole intact plants under variable climate conditions (NEDERHOFF and VEGTER 1994;

KÖRNER and CHALLA 2003; KÖRNER et al. 2007). In the present work, we therefore studied the effect of low night as well as very high day temperatures on CER on whole medium-sized tomato plants in order to evaluate the potential energy savings. Chlorophyll fluorescence measurements were included in order to detect any negative effects of the treatments on the efficiency of the photosynthetic apparatus.

2. Material and Methods

The experiments were carried out at the Centre for Plant Research in Controlled Climate, Ås (59° 40' N; 10° 46' E) in Norway. Seeds of tomato plants (*Solanum lycopersicum* cv. 'Mecano') were sown in peat in 10-cm pots, two seeds per pot. The pots were covered with transparent plastic sheeting until germination, and the weakest seedling was removed after germination. The temperature was 22/20°C during day/night. Supplementary light was applied at a photon flux density (PFD) of 200 μmol m^{-2} s^{-1} when global radiation was below 100 W m^{-2}. The plants were repotted twice, in a 3-liter container after the sixth leaf developed, and in a 10-liter container at a plant height of 1.5 m. A peat substrate (Veksttorv, Ullensaker Almenning, Norkisa, Norway) with a pH of 5.5-6.0 was used in the containers. The plants were watered with a mixture of 1:1 Superba Red and Calcinite (Yara International ASA, Norway) with a conductivity of 3.5 mS cm^{-1}. After the plants developed the second inflorescence, the plants were transferred to the experimental conditions. The plants were watered in the morning and in the afternoon until full saturation of the substrate in order to avoid any water stress. At end of the experiments, leaf area and the fresh and dry weight of the plants were recorded.

2.1. CO$_2$ exchange measurements

Gas exchange chambers were made using 1-mm thick, clear plastic with a light transmission of 95%. The diameter and height of the cylindrical gas exchange chamber was 70 cm and 200 cm, respectively. Two aluminum rings of the same diameter were used at the top and bottom of the plastic to maintain the cylindrical shape. The bottom of the cylinder was sealed tightly, while a hole in the top of the chamber functioned as an exhaust vent. An overpressure in the chamber prevented any uncontrolled leakage from the surroundings into the chambers. Each chamber was equipped with three heating units (each 200 W) in order to control night temperature in the chambers. The chambers were placed in a greenhouse compartment. Each chamber was connected to a 320 W electromagnetic air pump (Resun Model ACO-012A, China) 5 cm above the base. These pumps supplied either fresh air (about 400μmol mol^{-1} CO_2) or CO_2 enriched air to the chambers at an air flow rate of 210 liters per minute or 12.6 m^3 h^{-1}. An additional chamber was used to mix pure CO_2 from a bottle with fresh air in order to obtain the desired CO_2 concentration. It was accurately controlled by a constant air flow (electric air blower) and a capillary system for control of the CO_2 flow rate. The CO_2 concentration was thus controlled within ±10 μmol mol^{-1}. A diaphragm pump (12 V AC) built into the infrared gas analyzer (WMA-4 CO_2 analyzer, PP systems, Amesbury, MA, USA) sampled inlet and outlet air from each chamber (1 l min^{-1}) via flexible plastic tubing (4 mm internal diameter). Air from each sampling line was filtered by 1-3 mm granular silica (Merck KGaA, Darmstadt, Germany) filled in a 30-cm-long column, in addition to built-in hydrophobic air filter assembly, to ensure moisture-free clean air reached the infrared gas analyzer. Air sampling was regulated by a solenoid valve relay controller (AM416 Relay multiplexer, Campbell Scientific Inc. Logan, UT, USA) connected to a CR10WP data logger (Campbell Scientific Ltd, England, the UK). The light was measured using a quantum sensor (MQ-200 quantum sensor, Apogee Instruments Inc., Logan, USA). The sensor measured the light level every 30 seconds and recorded the means every 30 minutes. Air temperature (thermocouples) as well as air humidity (Vaisala HMP 35A sensor) were recorded in each chamber and the data stored in the Campbell logger.

System performance was tested by measuring the CO_2 exchange rate in empty chambers, and system error and carbon exchange caused by potting media (peat) was corrected by measuring carbon exchange rate for containing pots filled with similar quantity of media. Gradients for temperature and CO_2 along a vertical distance of 1.5 m was measured and minimized due to the high rate of air movement and turbulent mixing of air inside the gas exchange chamber.

The gas exchange was then calculated using this formula:

$$CER = \big((C_{in} - C_{out}) \times F\big) + \big((C_t - C_{t+20\,min}) \times V\big)$$

where C_{in} and C_{out} is inlet and outlet CO_2 concentration, respectively, F is the flow rate per 20 min, C_t and $C_{t+20\ min}$ the measured CO_2 concentration at time t and time t+20 min, respectively, and V the volume of the cuvette (HÖGLIND et al. 2011).

2.2. Experiment 1: The effect of different night temperatures on CER

The effect of three night temperatures (10.8±0.7°C, 15.0±0.9°C, and 18.1±0.7°C) on CER was studied at a PFD level of 200 µmol m^{-2} s^{-1} (11.5 mol m^{-2} day^{-1}) supplied by high pressure sodium lamps (Powerstar® HQI®-BT 400W/D, Osram, the Netherlands) 16 h day^{-1} (Experiment 1A). One plant was placed in each of three chambers, and all daylight was excluded by aluminized curtains. The day temperature was the same in the three chambers and varied between 20 and 23°C with a peak in the middle of the photoperiod (Fig. 1). The CO_2 concentration was 388±10 µmol mol^{-1}. The vapor pressure deficit (VPD) during the day was 700±150 Pa in the three different treatments. During the night, VPD was 410±170 Pa, 490±130 Pa, and 650±170 Pa for the low, intermediate and high night temperatures, respectively. The experiment was carried out over a period of 11 days. The total leaf area at the end of the experiment was 1.79 m^2 (21 leaves), 1.78 m^2 (21 leaves), and 2.12m^2 (22 leaves) for the plants grown at 10.8, 15.0, and 18.1°C night temperatures, respectively. Days were used as replicates.

In Experiment 1B, the effect of night temperature on CER was studied in daylight from 5 until 18 March. Supplementary light was given at a PFD of 200 µmol m^{-2} s^{-1} when the global radiation fell below 200 W m^{-2} (measured at the top of the greenhouse with a pyranometer CMP 6, Kipp & Zonen, Delft, the Netherlands, connected to a Priva greenhouse computer, De Lier, the Netherlands) within the photoperiod of 16 h. In this experiment, the number of chambers per treatment was extended to two because more chambers become available. The night temperature was 10.0±1.4°C, 13.3±0.4°C, and 18.3±0.7°C, while the day temperature varied between 20 and 26°C in all chambers (Fig. 2). The natural day length was 11-12 h, and the mean PAR was 15.5±2.7 mol m^{-2} day^{-1} including the artificial light. The CO_2 concentration was 415±8 µmol mol^{-1}. The plants were grown in peat in 5-liter pots. At the end of the experiment, the plants had 17.1 leaves in average, and the average leaf area of the plants was 1.18±0.11 m^2. Days were used as replicates. During

the day, VPD was 660±320 Pa and 760±480 Pa for plants grown under 10.0°C and 13.3°C, respectively. During the night, the corresponding VPD was 190±150 Pa and 260±140 Pa. An air humidity of 18°C was not available in this experiment.

2.3. Experiment 2: The effect of CO_2 concentration on CER under summer conditions

In the second experiment, four chambers were used with one plant per chamber (Experiment 2A). The experiment was carried out from 28 June until 13 July (16 days) at 398±31 µmol mol^{-1} CO_2, and a photoperiod of 17.5 h. In the presentation, days with very cloudy weather (maximum PFD <250 µmol m^{-2} s^{-1}) were excluded (total of 5 days). The mean maximum PFD during the days included was 924±175µmol m^{-2} s^{-1}, and the mean maximum temperature was 40.9±3.2°C (Fig. 2A). The mean PAR was 20.3±5.6 mol m^{-2} day^{-1}. The mean night temperature was 21.5±2.0°C. Vapor pressure deficit was 555±300 Pa during the day and 320±140 Pa during the night. The leaf area at the end of the experiment was 2.36±0.29 m^2, and the number of leaves was 23.

A similar experiment was carried out at 1016±99 µmol mol^{-1} CO_2 from 25 July until 1 August (8 days) (Experiment 2B). All days were included in the presentation of the results due to relatively sunny weather during this period. The mean maximum PFD was 1016±99 µmol m^{-2} s^{-1}, and the mean maximum temperature 44.6±2.5°C. The mean PAR was 22.8±2.8 mol m^{-2} day^{-1}. The mean night temperature was 21.5±2.0°C. The vapor pressure deficit was 550±360 Pa during the day and 210±140 Pa during the night. The leaf area at the end of the experiment was 2.37±0.24 m^2, and the number of leaves was 22.5±1.3.

2.4. Experiment 3: The effect of CO_2 concentrations on CER under early autumn conditions

The effect of CO_2 concentration (386±74 and 1009±64 µmol mol^{-1}) on CER was studied from 27 September until 9 October (12 days) in two chambers containing one plant each at both concentrations. Due to poor daylight conditions, four days were excluded from the presentation of the results. The mean maximum PFD was 626±121 µmol m^{-2} s^{-1}, and the mean maximum temperature was 35.8±3.4°C at low and 38.1±2.7°C at high CO_2 concentration. The mean night temperature was

18.5±2.5°C. The mean PAR was 10.2±2.8 mol m^{-2} day^{-1}.

The vapor pressure deficit was 540±260 Pa during the day and 410±160 Pa during the night at low CO_2 concentration, and 600±280 Pa and 360±170 Pa respectively, at high CO_2 concentration. The leaf area at the end of the experiment was 2.03±0.27 m^2 at low and 2.04±0.02 m^2 at high CO_2 concentration, and the number of leaves was 22.5±1.3 in both treatments.

2.5. Experiment 4: Chlorophyll fluorescence measurements

Plants from Experiment 1B that had been grown for 13 days under different night temperatures (10.0, 13.3, and 18.3°C) were used to measure chlorophyll fluorescence using a portable chlorophyll fluorometer (Plant Efficiency Analyser PEA; Hansatech Instruments, Norfolk, the UK). The two upper leaves of two plants per treatment were used. The fluorescence was measured after dark adaptation of 30 minutes and by using excitation light of about 1500μmol m^{-2} s^{-1}. The maximal photosystem II efficiency (F_v/F_m) was calculated according to Maxwell and Johnson (2000):

$$F_v/F_m = (F_m - F_0)/F_m$$

In addition, the maximum quantum yield (Φ_{PSII}) as well as the electron transport rate (J) were measured in plants from Experiment 3 grown under two CO_2 concentrations (385μmol mol^{-1} and 1000 μmol mol^{-1}) during 12 days with high maximum day temperatures. Plants kept in the greenhouse at 22±1°C/20±1°C day/night temperature at 400 μmol mol^{-1} CO_2 were used as control. Before measurement, the plants were adapted to the dark for ten minutes after a low-light period of 10μmol m^{-2} s^{-1}. The steady-state fluorescence was measured at a light intensity of 320μmol m^{-2} s^{-1}, and after 300 s, the minimum fluorescence level of the light-adapted leaf was measured immediately after the actinic light phase by illuminating the leaf with far-red light. Five measurements on the upper leaves of two plants per treatment were measured. The chlorophyll fluorescence was measured using a PAM2000 (Heinz Walz GmbH Mess- und Regeltechnik, Effeltrich, Germany).

The quantum yield of PS II electron transport (Φ_{PSII}) was calculated using the equation of Genty et al. (1989):

$$\Phi_{PSII} = (F'_m - F_t)/F'_m$$

The electron transport rate (J) was calculated using the formula of Genty et al. (1989):

$$J = \Phi_{PSII} \times PAR \times 0.5 \times 0.84$$

2.6. Statistical Analysis

Minitab 16 Statistical Software (Minitab Inc., 2010, State College, PA, USA) was used to analyze the results from Experiment 1-3 with a One-Way Analysis of Variance. The data obtained for chlorophyll fluorescence were analyzed using a General Linear Model. The regression analysis was done by using a Fitted Line Plot with CER as response and the light level as predictor in a Cubic Regression Model.

Results

3.1. Experiment 1

The effect of decreasing the night temperature from 18.1 to 15.0 or 10.8°C in Experiment 1A had no effect on CER during the light period when the plants were grown under 200 μmol m^{-2} s^{-1} PFD (Fig. 1). Relatively small differences were observed in respiration during the night between the treatments in this experiment. Similar results were obtained for a combination of daylight and artificial light (Experiment 1B), when the night temperature was decreased from 18.3 to 13.3 or 10.0°C (Fig. 2).Respiration was somewhat higher during the night in this experiment at 18°C compared to 13 and 10°C.

3.2. Experiment 2

The temperature in Experiment 2A (385 μmol mol^{-1} CO_2) increased progressively with increasing PFD levels (r = 0.895, p<0.001) as the light heated the chamber air (Fig. 3A). Since these two climate factors were closely interrelated, the correlation between PFD and CER (r = 0.892, p<0.001) was also reflected in the correlation between temperature and CER (r = 0.851, p<0.001). In the analysis, a one-hour delay was taken into account on the effect of PFD on recorded temperature. Maximum CER was reached at 400-500 μmol m^{-2} s^{-1}, PFD at a temperature of around 35°C, while a further increase of up to about 800 μmol m^{-2} s^{-1} PFD/41°C did not change the CER (Fig. 4).

The correlation between PFD and temperature in Experiment 2B (about 1000 μmol mol^{-1} CO_2) showed the same pattern as in Experiment 2A (r = 0.904, p<0.001). The correlation between PFD and

CER (r = 0.898, p<0.001), and temperature and CER (r = 0.887, p<0.001) was therefore quite similar. CER increased with increasing PFD and temperature up to the highest measured levels of about 1000 µmol m^{-2} s^{-1}/45°C. The maximum CER at high CO_2 concentration was almost double that reached at low CO_2 concentration (Fig. 3B and Fig. 4).

3.3. Experiment 3

In this experiment, PFD increased from 0 to about 550 µmol m^{-2} s^{-1} as the mean maximum level at the same time as the temperature increased from about 17°C to about 35°C (Fig. 5). At ambient CO_2 concentration, CER increased as the PFD/temperature increased up to around 400 µmol m^{-2} s^{-1}/30°C, while CER further increased up to a maximum of around 600 µmol m^{-2} s^{-1}/35°C (Fig. 5 and 6) at high CO_2 concentration. The maximum measured CER increased 90% as a result of CO_2 enrichment. There was a significant correlation between CER and PFD both at low (r = 0.914, p<0.001) and high CO_2 concentration (r = 0.937, p<0.001). As PFD and temperature were highly correlated (r = 0.912, p<0.001), CER and temperature were also closely related (r = 0.908-0.911, p<0.001).

3.4. Experiment 4

The maximum quantum yield (F_v/F_m) of plants grown at different night temperatures was found to be unaffected by decreasing the night temperature from 18.3°C to 13.3°C or 10.0°C (Table 1). The quantum yield of PSII (Φ_{PSII}) as well as the linear electron transport rate (J) were unaffected by high maximum temperatures both at low and high CO_2 concentrations (Table 2).

4. Discussion

The results clearly show that daily photosynthesis was not negatively affected by night temperatures of down to about 10°C. Photosynthesis in tomato plants exposed to 1°C for 16 h in darkness has been shown to be reduced by 37% when exposed to a subsequent light period (MARTIN et al. 1981). Tomato plants grown at a night temperature of 4°C for 10 h showed a negative effect on photosystem II, which reduced net photosynthesis (MARTINO-CATT and ORT 1992). It was concluded that such an effect can occur at temperatures of as high as around 10°C, but then only to a slight degree. It should also be noted that the accumulation of

photosynthetic end-products in the cells can result in reduced photosynthetic rates (GOLDSCHMIDT and HUBER 1992). Such a situation arises particularly when plants are grown under good light conditions at low temperatures. Long, dark periods with low temperatures in connection with a relatively low day temperature may thus result in end-product accumulation and reduced photosynthesis (PAUL et al. 1991; PAUL and FOYER 2001; HEINSVIG KJÆR et al. 2007). This was probably the reason for lower photosynthetic rates in tomato plants grown at 16°C/14°C (day/night) than in plants grown at 25°C/20°C (day/night) (VENEMA et al. 1999). In the present experiment in which day temperatures reached 23-25°C, resulting in a relatively high mean temperature, such negative effects did not seem to take place even at night temperatures down to 10°C. As CER was not affected, it was no surprise that the quantum yield as measured by chlorophyll fluorescence was also unaffected by the low night temperatures in the present experiment.

Increasing the irradiance level up to close to the maximum experienced in a greenhouse during summer at high latitudes (about 1000 µmol m^{-2} s^{-1} PFD), increased the CER despite temperatures rising up to 40-45°C as long as the CO_2 concentration was maintained at a high level. Although the CER increase stopped at a lower PFD level at ambient CO_2 concentration, a temperature increase of up to 40°C did not decrease the CER. Similar results were obtained under early autumn conditions although both the PFD and temperature reached lower levels. These results are in accordance with the conclusions of previous CER measurements in cucumber and roses (MORTENSEN and GISLERØD 2012a; MORTENSEN et al. 2012a). It therefore seems that the PFD level is the main factor determining the CER of the plants, and not the temperature within a certain range. As long as the CO_2 concentration is kept high, temperatures of up to about 40-45°C did not seem to pose any problem because of the high PFD level. At lower CO_2 concentrations, however, the negative effect of temperatures above 35°C probably counteracted the positive effect of an ever increasing PFD level. The positive effect of high CO_2 concentrations on photosynthesis is known to be related to a reduction in photorespiration in plants, a process that increases with rising temperatures (JOLLIFFE and TREGUNNA 1968; BROOKS and FARQUHAR 1985; URBAN et al. 2001). It is therefore generally accepted that the optimal temperature for photosynthesis is increased by CO_2 enrichment as well as by increased irradiance levels (JIAO et al. 1991; KIM and LIETH 2003).

Smillie and Gibbons (1981) showed that the maximum temperature for a detectable electron flow through photosystem II in tomato was 45.3°C. Murkowski (2001) found a decrease in photosystem II activity in tomato at 38°C. In the present experiment, the linear electron transport rate and the efficiency of PSII were unaffected by the high maximum temperatures as well as the CO_2 concentration, in accordance with the CER measurements that remained at the same level after several days of daily exposure to high temperatures. Heat damage on the photosynthetic apparatus depends both on light intensity and the duration of the high temperature (GEORGIEVA 1999). CAMEJO et al. (2005) found that tomato leaves that were treated for 2 h at 45°C showed a 50% reduction in the CO_2 assimilation rate. Taub et al. (TAUB et al. 2000) concluded that a high CO_2 concentration protects photosynthesis against high-temperature damage, and Percival et al. (1996) found that whole plants have a lower sensitivity to temperature than single-leaves. In the present experiments, including intact plants with 20-23 leaves, the duration of the very high temperatures was restricted to a relatively short daily period. An extension of this period, however, may have been injurious particularly to the plants grown at low CO_2 concentration.

It was recently found that maximum day temperatures of up to 32°C compared to 24°C resulted in the same total dry weight production when tomato plants were exposed to PFD levels of up to a maximum of about 1000 μmol m^{-2} s^{-1} in CO_2 enriched air (HÜCKSTÄDT et al. 2013). However, the marketable tomato yield was reduced by the high temperature probably as a result of an increase in the mean temperature. The high day temperatures should therefore be compensated by lower night temperatures in order to obtain an acceptable mean temperature. The present results indicate that this is possible as night temperatures down to about 10°C did not appear to have a negative effect on photosynthesis. This must, however, be tested in practice since high CER will not necessarily result in a higher yield and processes such as pollination and fruit development may be significantly affected (KHANAL et al. 2013b).

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Table 1. The maximum quantum yield (F_v/F_m) as affected by night temperature in Experiment 1B (n=4, ±SD).

Night temperature	F_v/F_m
10.0°C	0.77±0.03
13.3°C	0.76±0.02
18.3°C	0.77±0.04
Temperature	ns

Table 2. The maximum quantum yield (F_v/F_m), the linear electron transport rate (J), and the efficiency of photosystem II photochemistry (Φ_{PSII}) in plants exposed daily to high maximum temperatures at 385 µmol mol^{-1} (low) and 1000 µmol mol^{-1} CO_2 (high) in Experiment 3. Plants grown at 385 µmol mol^{-1} CO_2/20-22°C were also included (n=10, ±SD).

Treatment	F_v/F_m	J	Φ_{PSII}
Low temperature control	0.83±0.03	42.3±26.0	0.31±0.19
High max. temp./ low CO_2	0.84±0.01	41.3±11.5	0.31±0.09
High max. temp./ high CO_2	0.84±0.01	43.5±11.0	0.32±0.08
Temperature	ns.	ns	ns
CO_2	ns	ns	ns
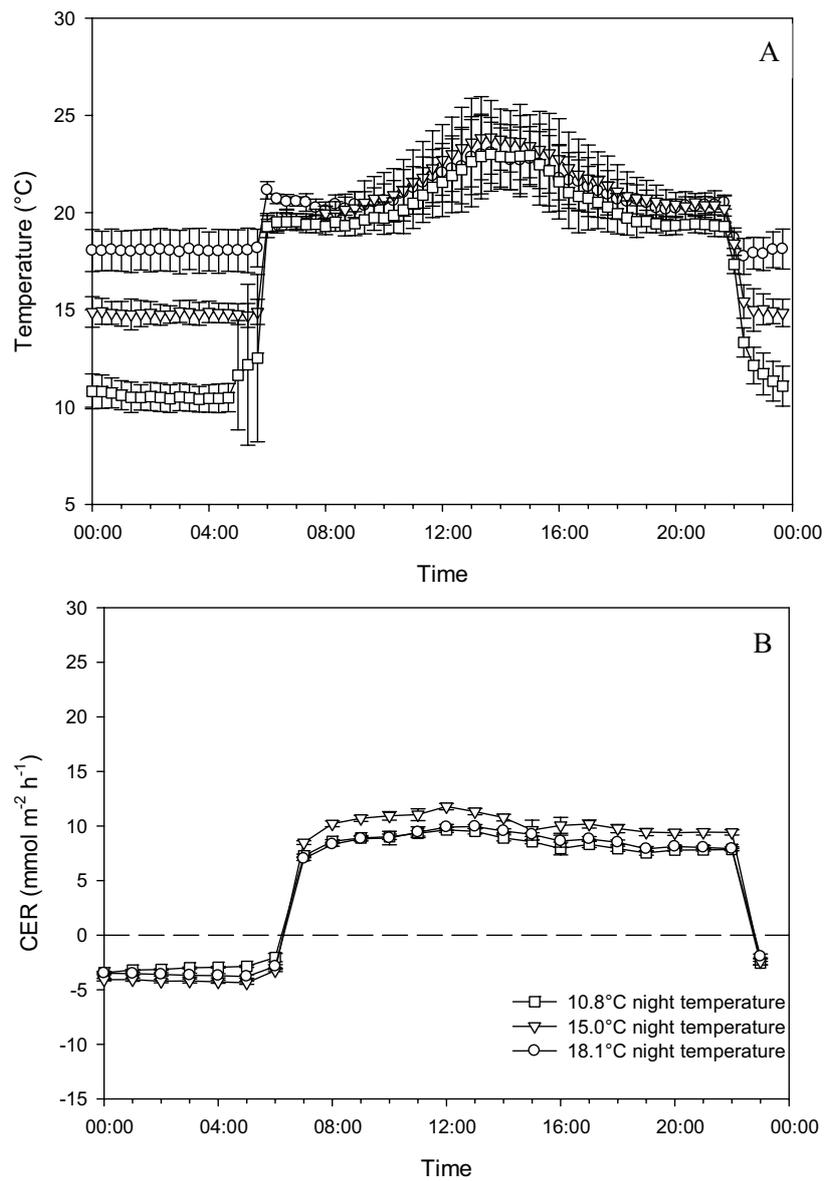
Figure 1. The temperature course (**A**) and carbon exchange rate (CER) (**B**) of plants grown at night temperatures of 18.1°C, 15.0°C, and 10.8°C under artificial light conditions of 200μmol m^{-2} s^{-1} PFD. Bars indicate Standard Deviation for the climate data and Standard Error for CER data, n=11.
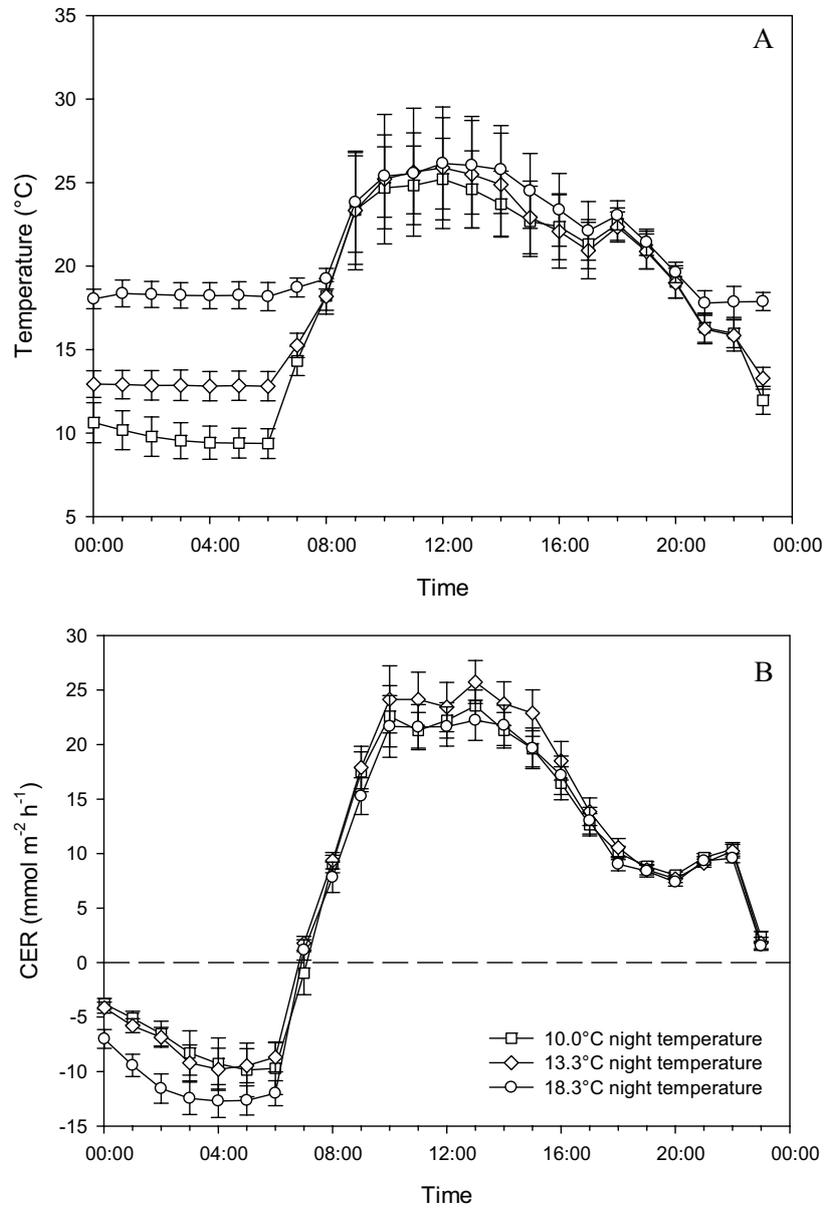
Figure 2. The temperature course (**A**) and the carbon exchange rate (CER) (**B**) of plants grown at night temperatures of 18.3°C, 13.3°C, and 10.0°C under natural daylight conditions with a daylight extension of HPS lamps. Bars indicating Standard Deviation for the climate data and Standard Error for CER data (n=28).
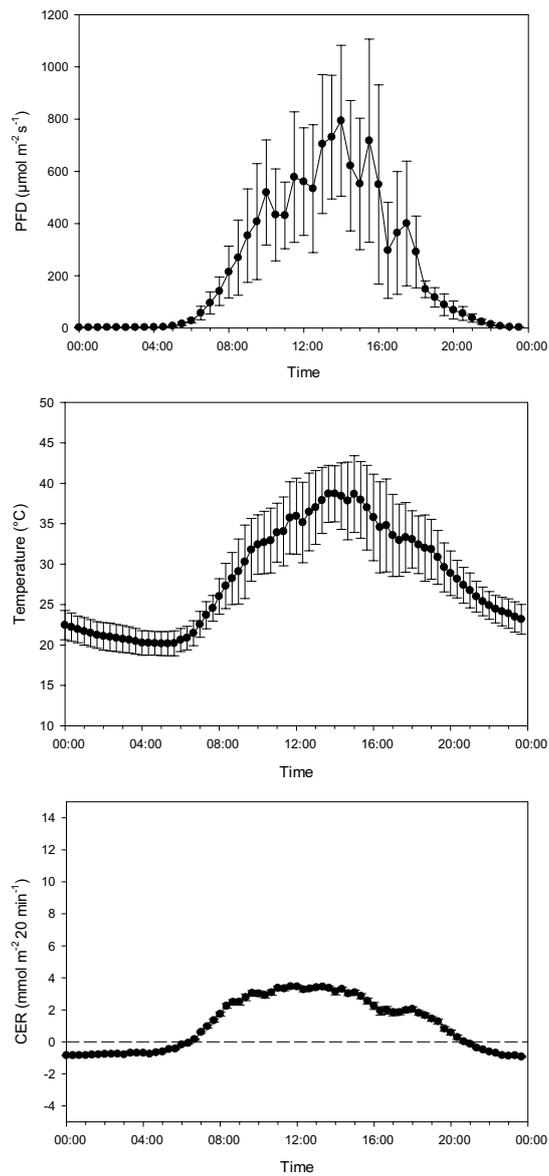
Figure 3A. Diurnal photon flux density (PFD), temperature and carbon exchange rate (CER) in mmol m^{-2} 20min^{-1} for plants grown under mid-summer conditions at ambient CO_2 concentration (398±31 µmol mol^{-1}). Bars indicating Standard Deviation for PFD and temperature and Standard Error for CER data (n=44).
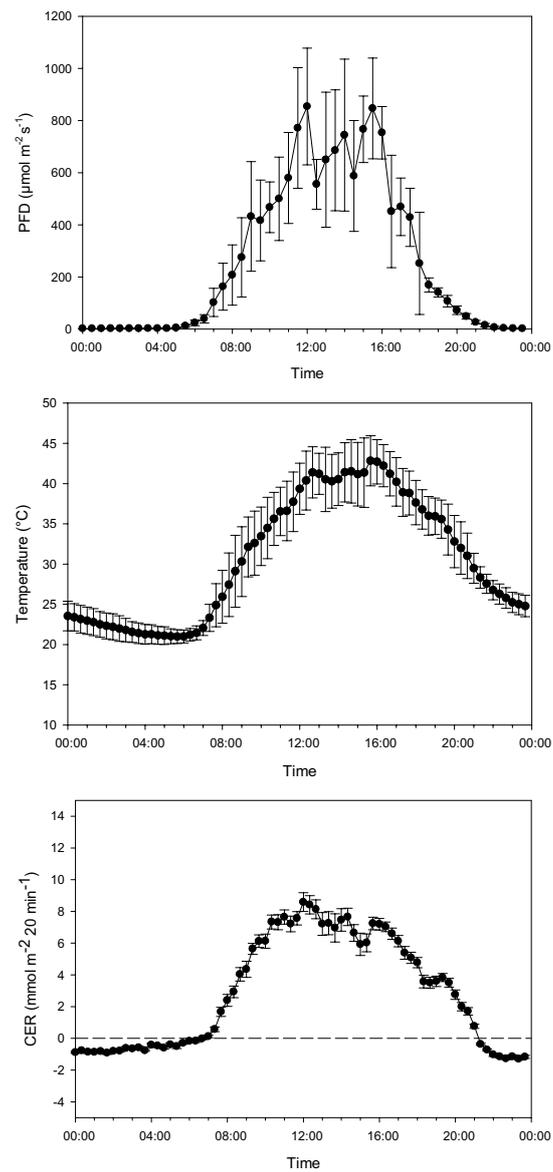
Figure 3B. Diurnal photon flux density (PFD), temperature and the carbon exchange rate (CER) in mmol m^{-2} 20min^{-1} for plants grown under mid-summer conditions at high CO_2 concentration (1016 ± 99 μmol mol^{-1}). Bars indicating Standard Deviation for PFD and temperature and Standard Error for CER data (n=32).

AJPS
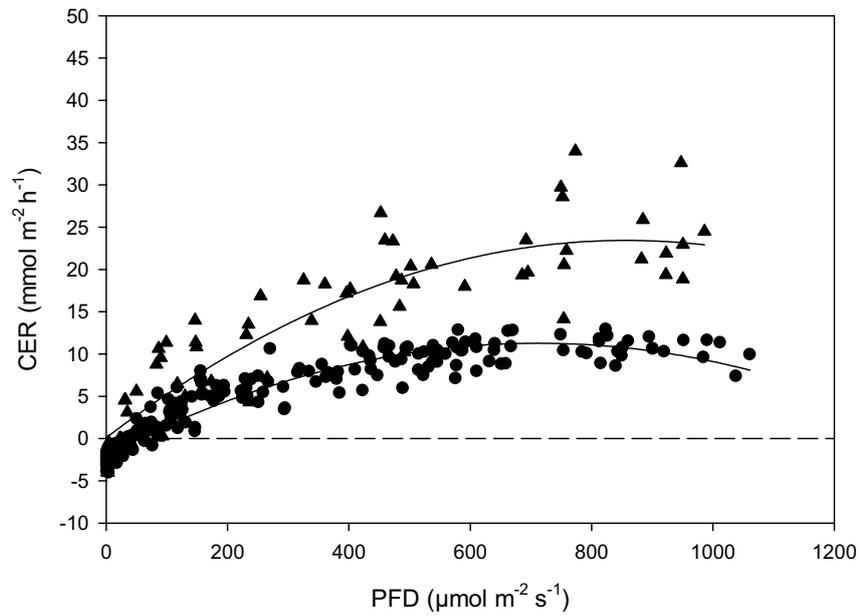
Figure 4. Relationship between photosynthetic flux density (PFD) and CER for plants grown under mid-summer conditions at ambient CO_2 (●, $R^2 = 0.931$) and at elevated CO_2 (▲, $R^2 = 0.881$).
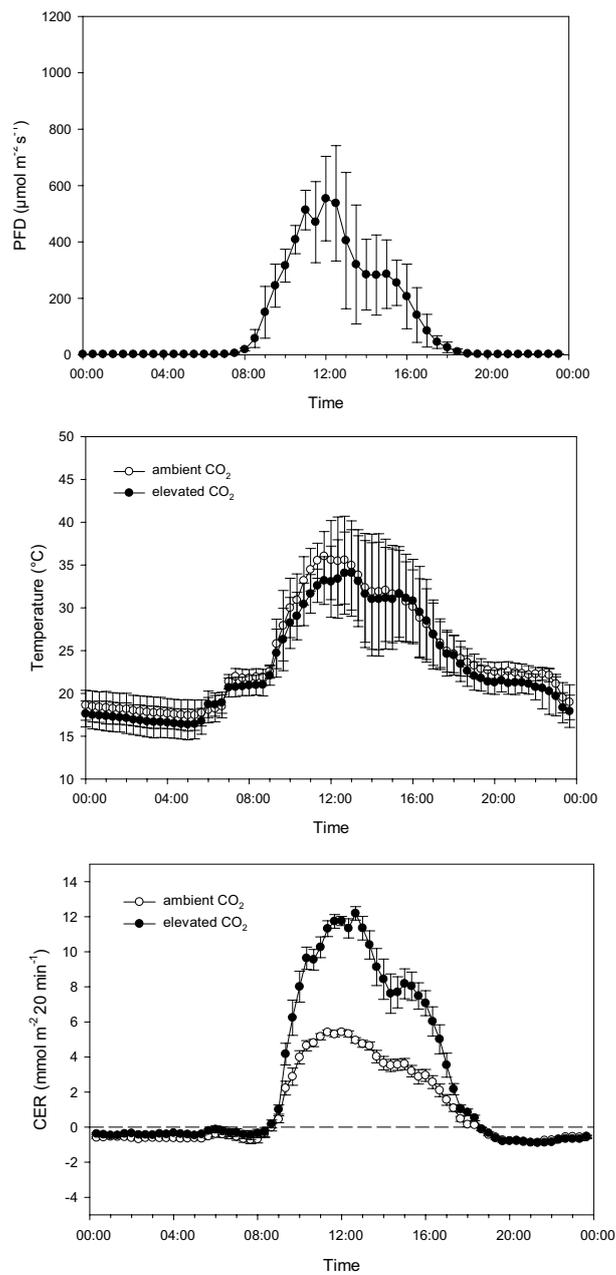
Figure 5. Diurnal photon flux density (PFD), temperature and carbon exchange rate (CER) in mmol m^{-2} 20min^{-1} for plants grown under early autumn conditions at ambient (386±74 μmol mol^{-1}) and elevated CO_2 level (1009±64 μmol mol^{-1}). Bars indicating Standard Deviation for PFD and temperature and Standard Error for CER data (n=32).
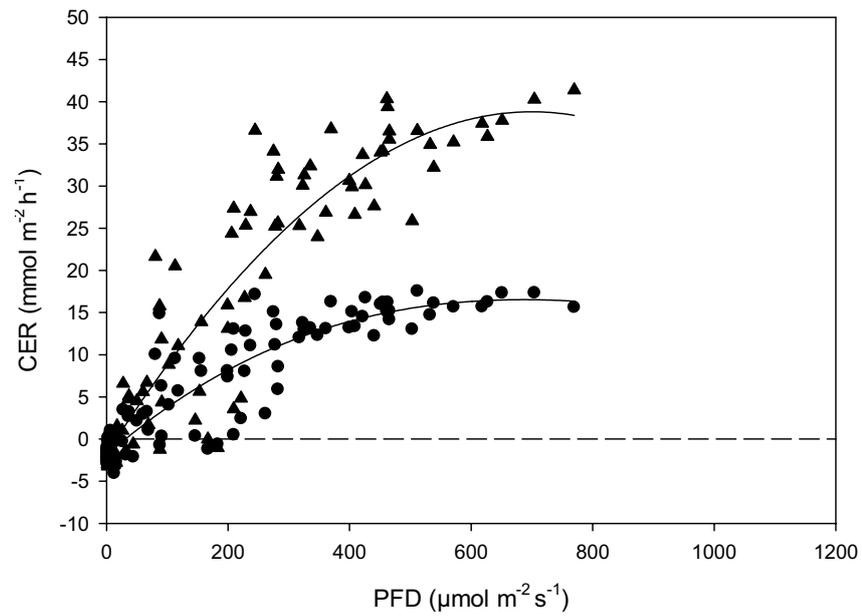
Figure 6. Relationship between photosynthetic flux density (PFD) and CER for plants grown under early autumn conditions at ambient CO_2 (●, $R^2 = 0.886$) and elevated CO_2 (▲, $R^2 = 0.914$).