THE EFFECT OF LIGHT QUALITY ON TOMATO (*SOLANUM LYCOPERSICUM* L. CV 'EFIALTO') GROWTH AND DROUGHT TOLERANCE

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Master's thesis

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Horticulture

2013

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Tiivistelmä — Referat — Abstract

Valon laadulla on todettu olevan vaikutus kasvien kasvurytmiin ja morfologisiin ominaisuuksiin. Aiemmissa valon laatua koskevissa koeasetelmissa auringon valospektriä on muutettu eri aallonpituuksia absorboivien kalvojen avulla. Tänä päivänä tutkimusta on aiempaa helpompi tehdä, sillä valon laatu voidaan nykytekniikalla tuottaa halutun laiseksi, eikä absorboivia kalvoja tarvitse käyttää. LED-valotekniikka mahdollistaa valospektrien valmistamisen kasvulle optimaaliseksi. Eri valospektrejä voidaan suunnitella yksittäisille kasveille tai kasviryhmille, riippuen viljelijän toiveista.

Tässä tutkimuksessa vertailtiin kuuden valospektrin vaikutusta tomaatin (*Solanum lycopersicum L.* cv 'Efialto') kasvuun, ilmarakojen toimintaan ja kuivuuden kestävyyteen. Kasvua verrattiin valokäsittelyjen välillä mittaamalla varren pituus, taimien tuore- ja kuivapaino, lehtipinta-ala ja lehtien lukumäärä, sekä lehtilapojen ja -ruotien pituus. Kuivuuskäsitellyille kasveille, joita oli kaikissa valokäsittelyssä puolet koekasveista, tehtiin vastaavat mittaukset.

Ilmarakojen toimintaa tutkittiin mittaamalla lehtilämpötilaa ennen kuivuuskäsittelyn aloittamista ja sen aikana. Lehtien epidermiltä mitattu lämpötila viittaa ilmarakojen toimintaan; mitä aukinaisempia ilmaraot ovat, sitä suurempi on haihdutus ja siten matalampi lehtilämpötila. Lehtilämpötilan mittaamisen lisäksi lehtien kaasujen vaihtoa mitattiin infra-puna laitteella, joka mittaa fotosynteesitehokkuutta sekä hiilidioksidin sitoutumiskykyä.

Punaisen ja kaukopunaisen valon suhde oli kokeessamme tärkein kasvien pituuskasvua ohjaava tekijä. Alhainen sinisen ja vihreän valon suhde edelleen edisti varren pituuskasvua. Pienikokoisten taimien todettiin kärsivän vähemmän kuivuuskäsittelyn aikana. Vihreän ja keltaisen valon todettiin säätelevän ilmarakojen sulkeutumista. Kuivuuskäsittelyn aikana valokäsittely, joka sisälsi eniten vihreää valoa, aiheutti ilmarakojen sulkeutumisen nopeimmin ja kaasujen vaihto laski eniten. Hyvän kuivuudenkestävyyden katsottiin johtuvan ilmarakojen sulkeutumisesta ja siitä johtuneesta haihdunnan vähenemisestä. Kuivuuden sietoon pystyttiin siis vaikuttamaan valospektrillä, säätelemällä kasvin morfologiaa ja ilmarakojen toimintaa.

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Plant growth and morphology can be manipulated with light. Previously light manipulation experiments were mostly conducted by modifying the solar spectrum with light absorbing filters. Today, research can be conducted with modern LED lighting techniques, which enables specific spectrum tailoring. Light can be tailored specifically for a species or a family, and the needs of the farmer can also be taken into consideration.

In this study, tomato (*Solanum lycopersicum* L. cv 'Efialto') seedlings were grown under six different spectra. Plant morphology, stomatal function and drought tolerance were measured. Growth measurements included stem height, plant fresh and dry weight, leaf - area and leaf number. In addition, the effect of light quality on leaf morphology was studied by measuring leaf blade and petiole length. All measurements were conducted on well-watered and water-stressed plants, in order to study the effect of drought on vegetative growth and drought tolerance.

Stomata conductance was studied by measuring leaf temperature prior to and during water stress. Leaf surface temperature indicates transpiration rate; thus the higher the conductance the lower leaf temperature. In addition to leaf temperature measurements, photosynthesis and stomatal conductance were measured by leaf level infra-red gas analysis.

R:FR ratio was the dominant factor for affecting plant morphology. However, the B:G ratio also played a key role; when the B:G ratio was low, it further enhanced the elongation growth, a response caused by low R:FR ratio.

Irradiance in green and yellow wavebands regulated stomatal closure. During water stress, the light treatment with the highest green irradiance, induced more rapid stomatal closure which was evident as increased leaf temperature and decreased gas exchange. Light-depenedent stomatal closure and decreased transpiration could explain the improved performance of these seedlings during the drought period. Light spectral quality thus affected the drought tolerance of tomato plants through its effects on plant morphology and stomata function.

1 CONTENTS

2   ABBREVIATIONS AND SYMBOLS

EC	Electric conductivity
LED	Light emitting diode
HPS	High pressure sodium
PAR	Photosyntetically active radiation
R	Red light, radiation between 620 and 750 nanometers λ
B	Blue light, radiation between 450 and 495 nanometers λ
G	Green light, radiation between 500 and 550 nanometers λ
FR	Far-red light, radiation between 710 and 850 nanometers λ
Pr:Ptotal	Phytochrome equilibrium; ratio between inactive phytochromes and the total phytochromes
ABA	Abscicid acid
CWSI	Crop Water Stress Index
λ	Wavelength

3 INTRODUCTION

Tomato (*Solanum lycopersicum* L.) is a plant species cultivated worldwide in greenhouses as well as in open fields. Tomato plants belong to the *Solanaceae* –family and produce fruit of different sizes and colours. In 2011, the world's tomato fruit yield was 159 million tons from 4 million hectares (FAOSTAT 2013). Tomatoes are popular for their versatile use when consumed fresh as well as their suitability for canning and sauce production.

In regions, where tomatoes are grown in fields, the seedlings are often pre-grown in greenhouses followed by transplanting. The transplanting process is a stressful event for small seedlings; stress can be caused by low soil and air temperatures (Melton and Dufault 1991), water deficit, soil salinity, and increased wind. In general, environmental stress causes growth retardation, a delay in flowering and fruit formation and thus potentially lower total yield. To overcome transplant stress, seedlings are required to be in good condition. High seedling quality can be achieved by managing the growth conditions in the greenhouse during the nursing period. Nutrition, temperature, water availability, and light conditions are known to have an effect on the stress tolerance of seedlings. Treatments, such as mild drought or chilling periods prior to transplanting, as well as chemical growth retardants have been used to reduce transplant stress in tomato plants (Latimer 1992).

Growers and consumers are willing to replace chemical growth retardants with more ecologically friendly solutions. An alternative to chemicals is provided by photobiology; plant growth manipulation is possible with light by using different wavelength combinations. In the horticulture industry, light in greenhouses has been manipulated for decades to produce better quality ornamentals and greenhouse vegetables (Kadman-Zahavi et al. 1976). Blue light is known to cause inhibition of stem elongation, whereas far-red (FR) enhances elongation growth of the stem and leaves. Today, LED technology provides a tool for growers to use tailored spectra for specific plant groups or species. By combining different wavelengths and creating new ratios between wavebands it is possible to enhance or retard growth and thus affect productivity. Furthermore, both reduction of the R:FR ratio and depletion of blue light are signals which induce a shade avoidance syndrome, such as shoot elongation and leaf hyponasty (Franklin 2008). There

is a lack of specific research on blue-light-regulated shade avoidance. It has been recently proposed that it would be worthwhile to investigate possible interactions between R:FR and blue light regulated shade avoidance, and how plants respond when these light treatments are combined (Keuskamp et al. 2012).

Many of the areas where tomatoes are cultivated are arid or semi-arid, suffering water deficiency and ground water salinity (Romero-Aranda et al. 2002). Tomato is relatively tolerant to saline soil conditions; however, excess salinity reduces plant growth and yield. Reduction of growth rate due to a saline environment is correlated to with decreased cell turgor. When the guard cells of stomata lose turgor, the stomata close and gas exchange slows down leading to decreased photosynthesis thus decreased growth rate. Abscisic acid (ABA) is a plant hormone which accumulates during drought periods and plays a key role in osmotic stress tolerance by regulating stomatal closure (Hayashi and Kinoshita 2011). Stomatal conductance is controlled by light and drought directly or mediated through abscicid acid.

The effect of light spectrum, especially different ratios between wavebands, on tomato seedling growth and drought stress tolerance was examined in this study. Growth and stress tolerance was evaluated by morphological measurements as well as ABA content, stomatal conductance, and photosynthesis measurements. When a tomato seedling is less susceptible to drought, it overcomes transplanting stress better, which is important for vigorous growth and yield formation.

4   PHOTORECEPTORS SENSE CHANGES IN LIGHT QUALITY

Being sessile, plants are constantly competing with other plants for light, living space, water, and nutrients. Competition for light causes morphological and developmental changes in plants (Franklin and Whitelam 2005). Plants have the ability to sense small changes in the spectrum, intensity and direction of light. Photoreceptors sense these light signals making possible the acquisition of information 'used' to adjust plant development. Three major groups of photoreceptors have been identified; red and far-red sensing phytochromes; UV-A and blue light sensing cryptochromes (Cashmore et al. 1999); and phototropins (Briggs and Huala 1999).

4.1   Phytochromes

Changes in the red:far-red (R:FR) ratio are detected by phytochromes. In *Arabidopsis thaliana* five phytochromes have been identified, phyA, phyB, phyC, phyD, and phyE (Franklin and Whitelam 2005). The tomato genome contains five identified phytochrome genes, *PHYA, PHYB1, PHYB2, PHYE,* and *PHYF*, which code PHY apoproteins (Alba et al. 2000). The R:FR ratio received determines the ratio between active and inactive forms of phytochrome (Franklin and Whitelam 2007). In darkness, phytochromes revert to their inactive state, Pr, which absorbs red light. When the inactive Pr absorbs red light, it converts to the active, Pfr, state. The active Pfr phytochrome absorbs far-red wavelengths; absorption of FR converts the Pfr back to Pr, thus the higher the R:FR ratio, the higher the Pr:Ptotal ratio.

4.1.1   Phytochromes and elongation growth

In nature, an equilibrium between Pfr and Pr exists, however the ratio of Pr:Ptotal decreases in shade conditions, due to the decrease in the R:FR ratio. In many species, the decrease in the R:FR ratio causes stem and petiole elongation, reduction in leaf thickness and chlorophyll content, and increased apical dominance (Franklin and Whitelam 2005). These symptoms can together be called as shade avoidance syndrome (SAS), and the function of elongating behavior is to achieve a better position for the plant to compete for

light. A prolonged period of low R:FR conditions leads to premature flowering and seed production; it is the plant's last attempt to reproduce (Halliday et al. 1994). Vegetation changes the daylight spectrum below a canopy, causing a decrease in the R:FR ratio. Red light is effectively absorbed by leaves, whereas far-red penetrates or is reflected through the canopy. Smith (1982) measured the R:FR ratio above and below canopy; above the canopy the R:FR was around 1.15 and below canopy it was only 0.05–0.7.

The five identified phytochromes (phyA-phyE) have been shown to play different roles in the shade avoidance response. Phy-B deficient *Arabidopsis* mutants grown under a high R:FR ratio have a similar growth habit to plants expressing the shade avoidance syndrome. It is therefore reasoned, that phyB is the main phytochrome involved in shade avoidance regulation (Franklin and Whitelam 2005). PhyA, on the other hand, is light labile; it is degraded in high intensity light and accumulated in etiolated seedlings (Quail 1994). PhyA has been shown to act antagonistically to phyB, since *phyA* mutants show shade avoidance symptoms in low R:FR conditions (Johnson et al. 1994). PhyA responds to far-red wavelengths whereas phyB responds to red wavelengths (Quail et al. 1995).

4.2   Cryptochromes

In 1993, the first gene coding for proteins with blue-light receptor activity, HY4, was identified and isolated from *Arabidopsis thaliana* (Ahmad and Cashmore 1993). Ahmad and Cashmore discovered, that the *hy4* mutant shows little, or no response to blue light. This unresponsiveness was evident as hypocotyl elongation during blue-light treatment. The insensitivity of the *hy4* mutant to blue light suggested that the cryptochrome pathway was incomplete. The researchers revealed that the HY4 gene encodes a protein similar in structure and sequence to the DNA photolyase (Ahmad and Cashmore 1993), the HY4 was later named as cryptochrome (Lin et al. 1996). DNA photolyases are enzymes, which repair damaged DNA. Cryptochromes are in fact flavoproteins, and despite their similar structure to DNA photolyases, cryptochromes do not share photolyase activity. Most cryptochromes are the blue- and UV-A –light receptors in plants (Cashmore et al. 1999).

4.2.1 Cryptochrome function and responses in plants

Cryptochromes are shown to be involved in photomorphogenetic responses, such as cell elongation, stem elongation inhibition, leaf expansion, entrainment of the circadian clock, gene expression, and photoperiodic flowering. Cryptochromes function together with red- and far-red wavebands absorbing phytochromes. (Lin 2002.)

The cry1 and cry2 of *Arabidopsis* have been shown to encode nuclear proteins; CRY2 is imported to the nucleus regardless of light treatment whereas CRY1 has been shown to be imported to the nucleus in the dark and exported from the nucleus or remain in the nucleus in the light (Cashmore et al. 1999). In the nucleus, the cryptochromes affect gene-expression in two ways: 1) direct binding between the cryptochrome molecule and a protein associated with the transcription pathway of a gene 2) the cryptochrome molecule binds to a protein, which has other cellular functions, such as degradation of proteins.

The functional mechanism of cryptochromes is reported to be more complicated than that of photolyases. During the activated signaling state of Cry1 and Cry2, the oxidized ground state of FAD absorbs blue light and induces the formation and accumulation of FADH·. Blue light signaling is reversed by green light, since FADH· absorbs green and causes its reduction to FADH⁻. In dark conditions FADH⁻ is returned to its fully oxidized form (Möglich et al. 2010). Thus the blue:green ratio affects the effectiveness of the total blue light received. In the paper by Sellaro et al. (2010), it was demonstrated, that decreasing the B:G ratio linearly resulted in hypocotyl elongation, a response mediated by cryptochromes. A picture of the cryptochrome's photocycle in blue and green light conditions is presented in Figure 1.
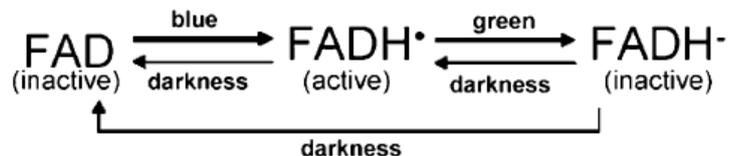
Figure 1 Cryptochrome's photocycle. In dark conditions, cryptochrome is in its oxidized form, FAD. Blue light drives reduction of FAD to the active form, FADH·. FADH· is further reduced to the fully reduced form of the chromophore, FADH⁻, by green light. In the FADH⁻ form, the receptor is inactivated, but reverts back to its active state in dark conditions. Figure: Folta and Maruhnich 2007.

As mentioned earlier, together with phytochromes, cryptochromes mediate photomorphogenic responses in plants. De-etiolation of a germinated seedling is a cryptochrome dependent response, which occurs when a seedling reaches the ground surface. During the de-etiolation process, continued elongation of the hypocotyl is inhibited and the cotyledons open (Lin 2002). The *cry1* mutant, previously called *hy4*, was shown (Ahmad and Cashmore 1993) to grow elongated seedlings when exposed to blue light; their unresponsiveness to blue light was due to a mutation in the CRY1 gene. Lin et al. (1998) conclude in their study, that cry1 and cry2 function simultaneously in the de-etiolation process when light intensity is low; if light intensity increases, cry1 is more dominant than cry2, and cry2 is eventually degraded. Lin et al. (1998) report that cry1 and cry2 act together with other photoreceptors, such as phyA and phyB, during de-etiolation process.

During blue light treatment, cry1 is transported to the cytosol, where it regulates the cytosolic and plasma membrane proteins (Lin and Shalitin 2003). It is known, that cryptochromes affect the anion channel activity of plant plasma membranes causing depolarization of the membranes (Spalding and Smith 2000). Depolarization of plasma membranes affects cell elongation, which leads to inhibited cell expansion and inhibition of stem elongation. Ahmad et al. (1995) report that, in addition to the hypocotyl elongation-inhibition response mediated by cry1, cry1 also has a key role in anthocyanin accumulation in plants.

4.3 Phototropins

Phototropins are blue light receptors, which regulate photo-induced movement in plants. Photo-induced movement includes chloroplast movement, phototropism, leaf expansion, and stomatal opening (Briggs and Christie 2002). Huala et al. (1997) studied phototropism in *Arabidopsis* using a mutant with impaired phototropism. They discovered that the *Arabidopsis* NPH1 gene responsible for blue light-mediated curvature contained a serine-theorine kinase domain in the C-terminus and LOV1 and LOV2 domains in the N-terminus. The gene NPH1 encodes a component acting in the phototropism signal-transduction pathway and this was later named as PHOT1.

Cry1 and cry2 have been shown to regulate random curvature of *Arabidopsis* hypocotyls in blue light, however specific bending towards a blue light source is mediated by phot1 and phot2 (Ohgishi et al. 2004). In the study by Ohgishi et al. (2004), phot1 and phot2 were shown to be responsible for chloroplast accumulation, whereas cry1 and cry2 caused no response. The researchers concluded that phot1 and phot2 function independently from other blue light receptors affecting stomatal movement and chloroplast accumulation. Cotyledon expansion under blue light conditions was also shown to be a phot1 and/or phot2 dependent event. However, hypocotyl elongation inhibition, anthocyanin accumulation, and cotyledon opening were shown to be cry1 –mediated events and occurring independently from other blue light receptors. Ohgishi et al. (2004) studied the blue light receptors using an *Arabidopsis* combinatorial multiple mutant (*phot1 phot2 cry1 cry2*). A blue-light-initiated, phototropin mediated, response, such as stomatal opening, can be fully reversed by green light (Frechilla et al. 2000).

5   WATER DEFICIT AND STOMATAL REGULATION

Plants suffer from water deficit during environmental stresses, such as high temperature, low temperature, salinity, and drought (Smirnoff 1993). Such stress is often evident as wilting symptoms. Wilting can be partially prevented by closing stomata, which inhibits excessive water loss by evaporation.

5.1   Water deficit

During water deficit, plant cell water potential decreases and stomata close. Stomatal closure results in reduced CO_2 uptake and therefore a decreased photosynthetic rate (Chaves 1991). Plant size, and especially the leaf area index (LAI), affect the plants' ability to cope in drought conditions; plants with small leaf area are more drought resistant than plants with large leaf area (Blum 2011). In addition, plants can be grouped into isohydric and anisohydric plants by their stomatal control mechanism (Tardieu and Simonneau 1998). Isohydric plants have a high control over the stomata during water stress and stomata close even when the leaf water potential is still high. Isohydric plants regulate stomatal opening via root-to-shoot signalling, including chemical (ABA) and

hydraulic interactions. On the other hand, anisohydric plants keep their stomata open longer than the isohydric plants during water stress; stomata of an anisohydric plant close only when the leaf water potential decreases significantly. The classification of plants to the two distinct groups is ambiguous; differences between species cultivars occur, which makes classification even more difficult. Sade et al. 2009 classified tomato in their study as an isohydric species.

A short, artificially created, water stress period prior to transplanting or during fruit ripening may improve the quality and stress tolerance of certain species. For example, a short water stress period at the time of fruit ripening has been used to improve the fruit quality, e.g. sugar concentration, of tomato (Shinohara et al. 1995). During water deficit, the water content of the fruit decreases, which causes an increase in the soluble sugar content, the plant also allocates its photosynthate to the maturing fruit during stress period. However, the total yield of tomato is decreased by both mild and intense water stress.

During water stress, the stomata close and carbon dioxide fixation is limited. When carbon dioxide is not fixed, chloroplasts are exposed to excess excitation energy (Smirnoff 1993). Energy from triplet-excited chlorophyll is transferred to oxygen, forming singlet oxygen, a form of reactive oxygen species harmful to plants. Reactive oxygen species (ROS), such as superoxide, hydrogen peroxide, hydroxyl radicals, and singlet oxygen, cause damage to plant cells. Damage can be evident as lipid peroxidation, denaturation of proteins, and damage to nucleic acids. In lipid peroxidation, the lipids break down, which leads to impairment of membrane function. Oxidation of nucleic acids and proteins leads to decreased catalytic activity and denaturation; damaged proteins are also more susceptible to degradation.

Plant cells have systems to either remove or repair the damage caused by ROS. When DNA is damaged due to ROS, DNA-repair enzymes activate. Under normal conditions, plants produce protective and repair systems which prevent oxidative damage. Superoxide dismutase (SOD), catalase, peroxidase, and ascorbate are examples of antioxidants, which react with ROS, so keeping the ROS levels low. Glutathione (GSH), glutathoine reductase (GR), and ascorbate are examples of compounds which regenerate oxidized antioxidants. Oxidative damage is likely in the photosynthetic cells, because of

their high oxygen concentration, high level of polysaturated lipids in the thylakoid membranes, and limitations on the pigments' ability to absorb excess light. The light absorbed by photosynthetic pigments is easily transferred to energy used to form ROS (Asada 2006). Short wavelength light contains the most photons and thus the most energy, which is why the UV-wavelengths are the most dangerous to plants. Short wavelength irradiation, UV-B and blue light induce phenolic compound accumulation into the epidermal cells. Flavonoids are the largest group of phenolic compounds; they protect the leaf surface layer by absorbing harmful wavelengths and act as antioxidants against ROS (Agati and Tattini 2010), for example by scavenging singlet-oxygen in chloroplasts (Agati et al. 2007).

5.2 Light mediates stomata movement

Each stoma has two opposing guard cells, which form pores in the leaf surface allowing CO_2 uptake and preventing excessive loss of water during drought. Stomatal density and stomatal activity affect rates of conductance; environmental factors such as CO_2, light, and humidity regulate stomatal movement. For example low CO_2 concentration in the sub-stomatal cavity causes stomatal opening. Guard cells sense environmental cues and change their shape and turgidity according to the surrounding conditions. The turgor of guard cells determines stomatal movement; osmosis drives water movement into and out of the guard cells. Turgor pressure is dependent on potassium ions (K^+) and sugars imported into the guard cells. (Blum 2011.)

Light is one of the environmental factors influencing guard cell turgidity. Blue light stimulates H^+ release from guard cells through electrogenic pumping by H^+ATPases leading to transient membrane hyperpolarization; H^+ATPase activity is increased by blue light. Hyperpolarization of the plasma membranes activates voltage-gated K^+ channels. These K^+ channels are ATP dependent and sensitive for Ca^{2+} (Shimazaki et al. 2007). ATPases, activated by blue light, pump H^+ resulting to an electrochemical potential gradient, which drives the movement of K^+ and Cl^- ions into the guard cells through ion channels (Tallman 1992), causing the guard cell osmotic potential to increase and water to flow into the guard cells. Karlsson (1986) studied blue-light-mediated stomatal opening in wheat and discovered that stomatal opening has an action spectra maximum at 450 nm

and two minor peaks of activity at 420 and 470 nm. Green light has been shown to reverse the effect of blue light on stomatal opening in pea (*Pisum sativum*) (Frechilla et al. 2000). In a study by Frechilla et al. (2000), a green light pulse lasting only 30 seconds reversed the stomatal opening caused by a previous blue light pulse. The stomata could be opened again with a subsequent blue light pulse. Frechilla et al. (2000), also noted that when blue and green light were given simultaneously, a B:G ratio of 1:2 completely inhibited the stomatal opening. Green light has since been shown to reverse blue-light-mediated stomatal opening in many species, such as *Pisum sativum, Commelina communis, Arabidopsis thaliana, Nicotiana tabacum*, and *Allium cepa* (Talbott et al. 2002), at a B:G ratio of 1:2. The green light effect has been shown to have an action spectrum with maximum at 540 nm and two minor peaks at 490 and 580 nm (Frechilla et al. 2000).

Blue light receptors, phot1 and phot2, are known to be involved in the regulation of stomatal movement and located in the plasma membrane (Kinoshita et al. 2001). Phytochrome-mediated and blue-light-dependent stomatal opening were studied with a wild-type (WT) genotype, *npq1* mutant and *phot1 phot2* double mutant, of *Arabidopsis thaliana* by Talbott et al. (2003). The *npq1* mutant fails to accumulate zeaxanthin, a chloroplastic carotenoid identified as one of the blue light photoreceptors in guard cells (Frechilla et al. 1999). Plants with a single mutation, either phot1 or phot2, have a normal phenotype, but the stomata of double mutants, *phot1 phot 2,* do not respond to low irradiance blue light (Talbott et al. 2003). In high irradiance blue light, the stomata of the double mutants opened; stomatal opening was reversible only with green light, indicating that stomatal response of the double mutant is blue light -dependent. The stomata in *npq1* mutant fail to respond to blue or green light (Frechilla et al. 1999, Talbott et al. 2003, Talbott et al. 2005).

5.3   Abscisic acid – a plant stress hormone regulating stomatal movement

In 1963, a plant hormone, Abscicin-ii, was discovered to cause fruit abscission (Ohkuma et al. 1963). Later in the 1960s, the hormone was also noted to cause seed dormancy, accumulate in wilting leaves, and induce stomatal closure. The hormone was found to accumulate during cellular dehydration periods, therefore the hormone was described as a "stress hormone" and its name was eventually changed to Abscisic acid (ABA). When

soil is dry and hard, ABA is formed in the roots, where it travels through the xylem into leaves. During drought, the xylem sap pH generally increases, which enhances ABA activity (Blum 2011).

ABA causes shoot growth retardation, which can be explained at least in part by a decreased photosynthetic rate resulting from stomatal closure. In addition to lowered photosynthetic rate via stomatal closure, ABA disturbs DNA synthesis by inactivating some DNA-replicon origins, resulting in inhibition of cell expansion and cell division, which is evident as shoot growth retardation (Blum 2011). However, root growth and root hydraulic conductivity are enhanced by ABA activity (Munns and Sharp 1993). ABA enhances aquaporin activity in the root zone which increases the root water flux. When shoot growth decreases and root growth increases, the root:shoot dry-matter ratio increases during water deficit. Higher root:shoot ratio is advantageous to plants during water stress, and may help survival through stress periods (Blum 2011).

ABA can be used as an exogenous spray-treatment prior to or during transplanting of vegetable seedlings to prevent severe water stress symptoms (Agehara and Leskovar 2012). Exogenous ABA treatment has been shown to maintain cells' water potential, reduce stomatal conductance, and photosynthetic rate during water stress. ABA reduces cell membrane damage, leaf abscission and improves overall seedling quality during and after transplanting. It must be taken into consideration that ABA temporarily reduces seedling growth; however, the effect is short-term and growth returns to normal quickly (Leskovar et al. 2008).

During drought periods, ABA has been reported to accumulate in leaves and especially into the guard cells of stomata (Shimazaki et al. 2007). ABA induces depolarization of the plasma membrane by inhibiting H^+ pumping by H^+ATPases (Hayashi and Kinoshita 2011). In addition to membrane depolarization, ABA activates anion-channels, such as K^+_{OUT}, leading to an anion efflux from the guard cells and therefore decreased turgidity. Stomatal closure by ABA is mediated via its secondary messengers, Ca^{2+} and NO (Garcia-Mata and Lamattina 2007).

5.4 Photosynthesis

Photosynthesis takes place in the leaf cells' chloroplasts, which contain pigments, such as chlorophyll *a*, chlorophyll *b*, and carotenoids. Photosynthesis includes light reactions and the Calvin cycle; light reactions that transform solar energy to chemical energy. The light reactions take place in chloroplasts, where solar energy is transformed to ATP and NADPH. Part of the ATP and NAPDH produced are used in the Calvin cycle, where CO_2 molecules are fixed (a process catalyzed by Rubisco), and later reduced to carbohydrate.

Pigments in the chloroplasts are able to absorb solar radiation between 380 and 750 nm, therefore called photosynthetically active radiation (PAR). The closer the waveband is to 380 nm, the more energy each photon has. Generally, the more the plant cells contain pigments, such as chlorophyll, the higher the photosynthetic rate is (Fleischer 1934). The absorption peaks of chlorophyll *a* are at 660 nm and 430 nm, and those of chlorophyll *b* at 640 and 450 nm, covering the red and blue waveband fractions of the PAR spectrum. The action spectrum of photosynthesis differs from that of the chlorophyll's, indicating that other pigments also harvest light and contribute to photosynthesis. These accessory pigments, such as beta-carotene, have absorption peaks in the green and blue wavelengths, resulting in more efficient photosynthetic capacity. The rate of photosynthesis is not dependent on the plant pigment content alone, but also on the plants' ability to bind CO_2 from atmosphere. The binding of CO_2 can be estimated by calculating the ratio between the CO_2 concentration in the stomatal cavity and the CO_2 concentration in the ambient atmosphere (Ci/Ca ratio).

Environmental factors, such as light and water deficit affect photosynthesis rate as well. Light and drought control stomatal movement, and thereby regulate the gas exchange and photosynthetic rate. The light quality also affects the photosynthetic rate; the better the irradiation matches with the chlorophylls' absorption peaks, the higher the photosynthesis rate. However, the photosynthetic rate is not only dependent on the red and blue wavebands, and higher photosynthetic rates have been also measured under light sources containing multiple wavebands (Yorio et al. 2001).

6 LIGHT MANIPULATION IN THE HORTICULTURE INDUSTRY

Greenhouse covers can change the composition and intensity of transmitted light (Rajapakse et al. 1999). The removal of certain wavelengths is of special interest to growers and researches, since the resultant change in light quality may enhance the quality or modify the morphological characteristics of cultivated plants. (Rajapakse and Shahak 2007). Technology today has created new possibilities to manipulate light quality and produce species-specific spectra for the horticulture industry.

6.1 Light manipulation with colored filters

Greenhouse covers transmit either all wavelengths or are designed to absorb certain wavelengths changing the composition of solar spectrum (Rajapakse et al. 1999). When the cover of a greenhouse is designed to change the spectral quality of transmitted light, the aim is often to modify plant morphology or affect flowering time. Already in 1976, Kadman-Zahavi et al. had discovered that removal of blue light from the solar spectrum caused stem elongation in tomato plants, whereas filters transmitting solely blue and red inhibited stem elongation and delayed flowering. Kadman-Zahavi et al. (1976) also observed, that tomato seedlings grown under filters with far-red transmitting characteristics, elongated and flowered early. Similar results were again observed in a study by Mortensen and Stromme (1987) with chrysanthemum, tomato and lettuce seedlings.

One of the aims of filtering studies has been the removal of far-red light, in order to decrease the need for chemical growth regulators (Rajapakse and Shahak 2007). Using different covers, it has been possible to increase the R:FR ratio, which decreases stem elongation (Rajapakse et al. 1999). In the 1980's, a $CuSO_4$ liquid filter was nominated as the best growth regulating cover for poinsettia (McMahon and Kelly 1990), chrysanthemum, tomato and lettuce (Mortensen and Stromme 1987), since it effectively reduced stem elongation and internode length. $CuSO_4$ covers did not however achieve popularity, because they were difficult to handle, expensive, and had phytotoxic properties which made their use hazardous (Rajapakse et al. 1999).

Cheaper, easier to handle, materials were developed to replace $CuSO_4$. Dyed, photoselective films made from plastic had promising results (Lia et al. 2000) and were tested by multiple research groups. These dyed photoselective films had red (A_R) and far-red absorbing (A_{FR}) qualities, which enabled their use to manipulate the R:FR ratio inside greenhouses (Lia et al. 2000). The more pigment was dyed into the film, the better it absorbed far-red. However, when more dye was added, the amount of PAR transmitted also decreased, which led to lower quality plants. Films, which absorbed only far-red and no red, transmitted PAR better and reduced stem elongation effectively. These A_{FR} films were proposed to replace the $CuSO_4$ covers (Lia et al. 2000). Covers which increase the R:FR ratio are still of interest to growers and available today from multiple providers and manufacturers. Growers are interested in replacing toxic chemicals with more environmentally friendly solutions; films of reasonable cost are recommended especially for organic growers (Rajapakse et al. 1999), who are not allowed to use chemical growth regulators. For conventional growers, the inconvenient delay in flowering caused by far-red absorbing films, and the short life span of the films themselves hinders their commercial use (Rajapakse and Shahak 2007).

6.2   Light emitting diodes enable specific light manipulation

Fluorescent, metal halide, high-pressure sodium (HPS), and incandescent lamps are the most commonly-used light sources in plant growing facilities. Even though they are used in plant cultivation, their original purpose was use in human lighting applications, which results in rather poor spectra for plant growth. The photoreceptors of plants and humans differ from each other significantly; therefore it is justifiable to conclude, that new solutions to provide a light source tailored to plants are needed (Bula et al. 1991). Today, however, multiple spectra are available especially in the fluorescent selection, which are especially developed for plant cultivation purposes. Fluorescent tubes are commonly used in growth chambers, in which the light intensity level is low, however they are not suitable for many greenhouse applications due to the low energy efficiency. At low energy costs, the most efficient current spectral manipulation is conducted with the light emitting diodes (LEDs). LEDs can be used to replace the fluorescent tubes in growth chambers, due to their better light output and lowered costs in cooling.

6.2.1 LED technology

The first light emitting diode (LED) was reported already a hundred years ago by Henry Josef Round. But it's only since the 1960's, that the development of LEDs finally started, when red LEDs were first used in commercial electronic devices, such as signal lights for TVs and remote controls. Since the 1990's, the development of LEDs has been fast and today they are discussed as potential replacements for conventional lighting sources in greenhouses and other plant cultivation applications (Pinho 2008).

A light emitting diode is a semiconductor, containing two types of layers compressed to each other to create a positive-negative (p-n) junction. When a high enough voltage is applied to a diode, electrons from one layer move to the other and release energy in the form of a photon. When a photon of a certain energy is released, light is emitted at a certain wavelength. With LED technology, it is possible to create monochromatic light and a specific spectrum using different waveband combinations. Today, single, high-power LEDs, which emit at multiple wavebands, are available to the horticultural industry (Pinho 2008). These full-spectrum LEDs are more expensive and complicated to build, however they are already manufactured by some LED companies for commercial use. The long life span of LEDs is an advantage when compared to conventional HPS lamps, in addition to the fact that the LEDs do not emit as much directional heat towards the plants (Morrow 2008). The low heat-emitting character of LEDs allows the luminaires to be placed near plants and this facilitates interlighting between and within rows (Massa et al. 2008).

LEDs are considered to be energy efficient, however, today the energy consumption of LEDs differs only a little from that of HPSs, but the technology is evolving rapidly in favour of LEDs (Pinho 2008). Growers and consumers are interested in new, ecologically friendly, energy saving and long lasting products (Pinho et al. 2012). LEDs are promised to last almost twice the number of lighting hours of HPS lamps (Pinho 2008).

6.2.2 Research and LEDs

The red and far-red light photoreceptor, phytochrome, has two forms, the inactive Pr and active Pfr, which have absorption peaks at 660 nm and at 730 nm, respectively (Hiltbrunner et al. 2007). Phytochromes, together with cryptochromes mediate photomorphogenesis in plants; therefore the study of the wavebands of light is important. By taking into account the absorption peaks of photoreceptors when choosing light spectral quality, more desirable growth responses can be achieved. However, previously the response to a specific waveband was difficult to examine under realistic growing conditions, since electric lighting systems usable for plant cultivation contained more than one waveband. To create a certain spectrum, filters have been used to remove wavebands from the original spectrum of the light source.

Because the absorption peaks for red light photoreceptors were known, LEDs were first exploited because of their ability to create red light (Pinho et al. 2012). In the 1990's, red diodes with a peak emission at $\approx$ 660 nm were developed to match the action spectrum of phytochrome, for use in horticultural applications. However, the quality and radiation output of the first LEDs varied widely from 70 to 540 $\mu mol \cdot s^{-1} \cdot m^{-2}$ when measured at 1 cm from the LED chip (Bula et al 1991). One of the first plant-related LED experiments was conducted by Bula et al. (1991), who discovered that red LEDs enhanced the growth of lettuce when used together with white fluorescent tubes. Blue LEDs had not yet been invented in the early 1990s; therefore white fluorescent tubes were used to add blue light to the growth spectrum. Red light together with the fluorescent tube increased the biomass and reduced stem elongation of lettuce (Bula et al. 1991, Hoenecke et al. 1992). For a long time, research focused only on red and later blue regions of the visible spectrum (Pinho et al. 2012). The projects, e.g. Bula et al. (1991), and many similar studies from that time, were supported by NASA. NASA has continued to contribute to LED research from the 1980's to the present day. It was, and still is, in NASA's interest to find a good quality light source, which is energy efficient, produces less heat, and is well suited to growing edible plants under extra-terrestial conditions (Herridge 2012).

Studies of specific wavebands and plant responses are facilitated by tools like the LEDs. For example, the effect of green light on photomorphogenesis was previously little studied, due to difficulties in the technological aspects of the experimental design.

However, high powered LEDs with narrow wavebands have offered a solution to this problem, and today multiple studies on green light have been conducted and research in this area has recently made major progress (Folta and Maruhnich 2007).

6.2.3 Horticultural applications

Growers and researchers have been manipulating greenhouse light conditions with filters or covers since long before LEDs were available. Covers and filters are useful tools; however it is difficult to create specific spectra with them, also the intensity of irradiance transmitted decreases when light is filtered through a plastic or a liquid layer. Assessing the response to a specific waveband with filters and covers is more complicated than with LEDs. Furthermore, LEDs can provide a specific spectrum customized to the plant's needs. (Pinho et al. 2012.)

Today HPS lamps are used with nearly all plant species grown in greenhouses, however, their spectrum is not suitable for all plants. The HPS spectrum is high in yellow and orange wavebands, and the portion of blue light is small; this spectral distribution together with the high radiant heat peak causes an elongated growth and flowering response in many species (Brazaityte et al. 2010). One of the main benefits of LEDs, when compared to other light sources, is the possibility to create a customized spectrum. With a spectrum customized to a specific species or a plant family, the size, uniformity, and quality of yield can be better controlled. Growers would like to affect plant morphology as well as growth rate and time of flowering (Pinho et al. 2012). With blue light, it is possible to produce a compact growth habit, whereas green and far-red wavelengths cause elongation growth and flowering (Zhang et al. 2011, Hoenecke et al. 1992, Franklin and Whitelam 2005). When designing a spectrum, the ratio of different wavelengths is critical; the ratio between blue and green determines how strong the blue light responses are in a plant (Möglich et al. 2010), the red:far-red ratio influences elongation and flowering of plants (Franklin and Whitelam 2005). Therefore, one spectrum for all plant species is not enough, instead particular spectra are required that are suitable for ornamentals, or spectra tailored for leafy vs. fruiting vegetables, and naturally there is scope for further fine-tuning within these two groups.

LEDs provide a light source with less radiant heat output, which makes them suitable for plant factories where no natural light is available. Due to their low heat output, it is possible to place LEDs near the canopy, which enables multiple layer cultivation. In multiple layer cultivation, plants are cultivated on top of each other; this leads to an efficient use of space and thus saves in energy costs and increases yield per square meter (Morrow 2008, Pinho et al. 2012). Low heat output also decreases the need to ventilate the greenhouse (Pinho et al. 2012). When less ventilation is used, the CO_2 concentration remains high in the greenhouse; high CO_2 concentration increases photosynthesis and therefore growth and yield of horticultural crops (Kramer 1981, Daugovish et al. 2009).

It is speculated that LEDs will replace conventional lighting in the future (Pinho et al. 2012). High pressure sodium lamps (HPS) are currently widely used in greenhouses, however they are liable to break when switched on and off frequently. LED technology makes quick on-off switches possible, which is important when weather conditions are changeable. On a sunny day the lights can be switched off quickly, and on the other hand the lights can be switched back on, as clouds pass overhead, to ensure good growth without reducing the lifespan on the lamps.

LEDs are relatively expensive, when compared to the traditional HPS lamps or fluorescent tubes, therefore HPS lamps are still widely used in greenhouses and fluorescent tubes in tissue culture applications. Due to their high price, LEDs were previously used primarily in research facilities, but today they are becoming more and more common in horticulture where knowledge of their technical advantages has expanded and their price is decreasing (Morrow 2008).

The horticulture industry, together with the agriculture industry, is in charge of feeding the increasing world's population. Not only the increasing population, but also the increase in fossil fuel prices has put pressure on the horticulture industry. Greenhouses are not energy efficient at the moment; LEDs can provide relief to some extent. However, I believe that the current one-layered greenhouses are not the answer, but that the future of food production will be inside food factories, where food is produced in multiple layers with high powered, species specific customized LED lights.

7   AIMS

The aims of this study can be divided into two sections; firstly, the effect of different light quality were studied, secondly, whether the drought tolerance of tomato seedlings could be improved with a light treatment.

7.1   Light quality effects on seedling morphology, photosynthesis, and stomatal conductance

While knowing that growth manipulation is possible with different waveband combinations, one of the aims of this study was to test the effect of different light spectra on tomato seedling growth and seedling quality. The ratios between blue and green, and red and far-red light were of particular interest. The aim was to record the morphological effects caused by different spectral composition treatments produced by lamps in a greenhouse. Morphological measurements were conducted at the end of the experiment by measuring the height, fresh weight, leaf-area, leaf shape, and dry weight of the shoots. The hypothesis is, that shoot elongation will be inhibited with high R:FR and high B:G ratios. The generative growth stage was evaluated at the end of the experiment by counting the number of flower buds produced. The hypothesis is, that the number of flower buds will increase with increasing FR.

Blue light is known to enhance the compact growth habit of plants, whereas green wavebands cause elongation of stem and petioles. It has been discussed, whether the amount of blue wavebands in a spectrum itself, or the blue:green ratio, provides more information to the plants about their surrounding conditions e.g. shading (Sellaro et al. 2010). Sellaro et al. 2010, also claim that hypocotyl elongation is more controlled by the R:FR ratio than B:G ratio. Having six different spectra in our experiment, this hypothesis could be tested, and the limits of R:FR and B:G which affect hypocotyl elongation could be estimated.

Light quality, and especially the light spectrum, controls stomatal movement in plants. Blue light controls the opening of stomata via phototropins (Briggs and Christie 2002); green light has been shown to act antagonistically to blue light by closing the stomata

(Frechilla et al. 2000). Stomatal function and guard cell movement can be approximated by measuring leaf temperature; when stomata are open, the leaf surface is cooled by more evapotranspiration than when stomata are closed. In this study, we will study the effects of six different spectra on plant water relations. The consequences of differences in transpiration related to stomatal conductance will be measured using a leaf infra-red thermometer and a thermal camera, as well as direct measurements of gas exchange by the experimental plants using infra-red gas analysis. The hypothesis is, that leaf temperature will be higher under lights, which are rich in green and low in blue light.

7.2 Light quality effects on water deficit tolerance

The morphological measurements were performed on normally irrigated plants and plants subjected to a water deficit treatments, in order to demonstrate the effect of drought stress on tomato plant growth. The aim was to assess, how light quality affected the plants' response to water deficit.

Water deficit tolerance depends on many things, one is the size of the plant (Blum 2011); plants with smaller leaf area tolerate water stress better. In general, a smaller leaf area means fewer stomata and therefore less transpiration overall. Light quality affects cell growth and division rate and therefore also the leaf area; blue and red wavebands are known to enhance compact growth habit, whereas green, far-red, and yellow wavebands are connected to stem and petiole elongation. The effect of light quality on the plant morphology and leaf area and therefore water stress tolerance will be evaluated in this experiment with six different light spectra. We expect, that plants with smaller leaf area tolerate drought better than plants with larger leaf area.

Light quality does not only affect the morphological features of the plant, but also the water relations. Blue and green wavebands regulate the stomatal opening, which in turn correlates with stomatal conductance and transpiration. We expect to see, that plants with lower evaporation during water stress lose turgidity slower and are therefore more likely cope better during water stress.

During water deficit, plants synthesize compounds, which either control the stomatal conductance or act as antioxidants against reactive oxygen species (ROS). We expect, that an increase in the total upper epidermal flavonoid content during water stress improves the stress tolerance of the plants. The concentration of abscisic acid (ABA) in tomato leaves was measured from normally irrigated plants and from plants subjected to a water deficit treatment at the end of the experiment. The hypothesis is, that plants with the highest increase in ABA and total epidermal flavonoid content due to drought have lower stomatal conductance and cope well under drought conditions.

8 MATERIALS AND METHODS

8.1 Plant material and growing conditions

The experiment was conducted in a greenhouse compartment at the Viikki Greenhouse and Field Station, University of Helsinki, Finland (60º13'30" N, 25º2'0" E) during January and February of 2013. The greenhouse was covered by a glass roof and transparent double layered polycarbonate walls. Greenhouse temperature was set to 22 ºC (day) and 20 ºC (night). Temperature was controlled by the greenhouse environment control system (Priva, De Lier, Netherlands) and photoperiod was set to 18 hours. A shade screen was deployed constantly, regardless of solar radiation, in order to minimize the effects of changes in natural day light in the experimental 'plots'. The 12 experimental plot units were separated from each other with white/black plastic sheets on all four sides, with the white side of the film facing the plants, to prevent radiation passing between compartments. Relative humidity in the greenhouse compartment fluctuated between 40 and 60 % and was not controlled.

The tomato (*Solanum lycopersicum* cv 'Efialto') seeds were provided by Enza Zaden (Enkhuizen, Netherlands). Efialto is recommended as a rootstock variety for vigorous cultivars. A scion, a more productive and tasty variety is typically grafted into the rootstock when the seedling is 2–4 weeks old. Grafting is used to enhance resistance to soil borne pathogens, increase yield and to improve the resistance of the seedlings to harsh environments (Kubota et al. 2008). Seeds were sown on the 21st of January 2013 into rockwool cubes (Cultilene 100mm x 100mm x 65mm), one seed per cube. Cubes were thoroughly watered and placed under a black-and-white plastic sheet cover. After three

days, the seeds had germinated and the plastic cover sheet was removed. Cubes were placed under the different light treatments; 16 cubes in each treatment side by side in the middle of the experimental plot.

A trickle irrigation system was turned on four days after sowing (Figure 2); irrigation was done automatically with a nutrient solution of 1.8 mS/cm for four weeks, the fertilizer used was Kukkasuperex (N-P-K 11-3-26) made by Kekkilä (Vantaa, Finland). After four weeks, the conductivity level (EC) of the nutrient solution was raised to 2.5 mS/cm. The seedlings were irrigated with 0.5 dl of nutrient solution three times a day (07.30, 13.30, 19.30), making a total of 1.5 dl per day. The nutritional status of the cubes was dependent on the concentration of nutrient solution applied and the plants' ability to uptake nutrients from the rock wool cube. The nutrition status of the cube was monitored weekly but not controlled. The temperature of the rock wool cube was monitored weekly in order to document the ambient temperature differences between compartments. Air temperature differences between compartments were not monitored. Measured electrical conductivity (EC) values are presented in Table 1 and cube temperatures in Table 2.
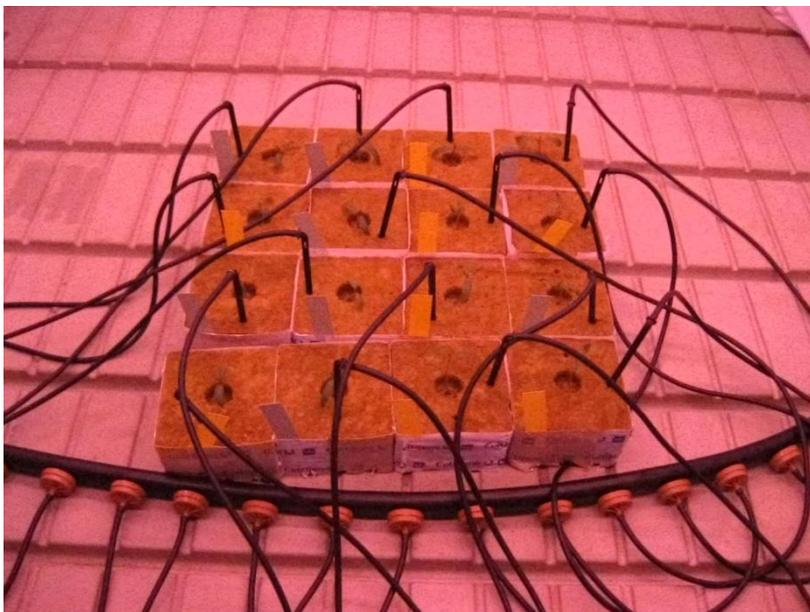
Figure 2 The 16 rock wool cubes placed side by side; each cube has its own irrigation tube. The cubes were drawn apart according to the growth rate of the plants. A yellow label in the cube: water deficit treatment, a green label: normally irrigated plants. Picture is taken from treatment AP67. Photo: Stiina Kotiranta.

Table 1 Electrical conductivity (EC) prior to and during water stress treatment in light treatments AP67, AP3, AP9, AP67B, AP673L, and HPS. Values are means of four measurements per light treatment. Wet = measurements from normally irrigated cubes, Dry = measurements from drought treated cubes.

	Measurement date									
Treatment	29.1.	4.2.	11.2.	19.2.		21.2.		22.2.	
	Wet	Wet	Wet	Wet	Dry	Wet	Dry	Wet	Dry
AP67	1.1	1.7	1.7	3.2	3.0	2.9	4.7	4.2	3.0
AP3	1.2	1.6	2.0	3.4	3.1	3.4	3.4	4.3	4.8
AP9	1.2	1.7	1.9	3.3	3.1	3.2	5.5	3.2	4.9
AP67B	1.3	1.8	1.9	3.2	3.4	3.1	4.4	3.3	3.7
AP673L	1.3	1.7	1.8	3.6	2.9	4.6	3.9	4.1	4.1
HPS	1.1	1.8	1.9	3.9	4.0	3.9	3.3	4.0	4.5

Table 2 Temperature in the rock wool cube (ºC) prior to and during water stress treatment in light treatments AP67, AP3, AP9, AP67B, AP673L, and HPS. Values are means of four measurements per light treatment. Wet = measurements from normally irrigated cubes, Dry = measurements from drought treated cubes.

	Measurement date					
Treatment	29.1.	11.2.	21.2.		22.2.	
	Wet	Wet	Wet	Dry	Wet	Dry
AP67	18.7	19.6	19.8	19.5	20.0	19.8
AP3	19.2	19.4	20.2	20.5	22.2	20.1
AP9	18.9	18.8	19.6	19.6	19.4	19.7
AP67B	18.8	18.1	19.4	19.6	18.5	19.6
AP673L	18.9	18.3	20.3	20.4	20.7	20.4
HPS	19.7	19.3	20.7	20.5	21.0	20.5

8.2 Light treatments and experimental design

Six different light treatments were tested; the experiment included two replicates of each treatment. The arrangement of the replicates in the greenhouse compartment was randomized. A map of the experimental layout is presented in Appendix 1.

In all of the 12 experimental plots the light intensity was set to ~150 μmol$\cdot$m$^{-2}\cdot$s^{-1}, the photon flux intensity was measured on the surface of the rock wool cube with an Ocean Optics spectrometer Jaz (Dunedin, Florida, USA). In treatments AP67, AP3, AP9, AP67B and AP673L, the light sources used were LED lamps (lamp type B100, Valoya Oy, Helsinki, Finland). One treatment was conducted with 400 W high pressure sodium lamps (HPS) (Philips, Eindhoven, Netherlands), photon flux intensity level was set by adjusting the distance between luminaires and rock wool cubes.

Each treatment had a different spectrum; the nanometer distribution at 50 nm intervals as percentage from the total (400–800 nm) spectrum, red:far-red (R:FR), blue:green (B:G), blue:photosynthetically active radiation (B:PAR), green:PAR (G:PAR), red:PAR (R:PAR) photon ratios, phytochrome equilibrilium (Pr:Ptotal), and estimated CRY2 effective photon irradiance of each spectrum is presented in Table 3. The R:FR, B:G, B:PAR, G:PAR, R:PAR photon ratios were calculated according to the definitions for different light colours by Sellaro et al. 2010; R:FR = (650–670 nm)/(720–740 nm), B:G = (420–490 nm)/(500–570 nm), B:PAR = (420–490 nm)/(400–700 nm), G:PAR = (500–570)/(400–700 nm), R:PAR = (650–670nm)/(400–700 nm). The phytochrome equilibrium, Pr:Ptotal, was calculated with R version 3.0.1 with photobiologyPhy - package (Aphalo, 2013a), and CRY2 effective photon irradiance with photobiologyCry - package (Aphalo, 2013b).

Table 3 The spectral distribution at 50 nm intervals as percentage from the total (400–800 nm) photon irradiance, R:FR, B:G, B:PAR, G:PAR, R:PAR, Pr:Ptotal, and CRY2 effective photon irradiance in light treatments AP67, AP3, AP9, AP67B, AP673L, and HPS. PAR is photosynthetically active radiation. NA = not available.

Wavelengths		AP67	AP3	AP9	AP67B	AP673L	HPS
400–450nm		6.4	13.2	34.4	0.1	7.9	1.5
450–500nm		5.3	7.1	19.4	0.1	4.9	3.8
500–550nm		6.5	16.5	0.2	6.0	3.5	2.1
550–600nm		9.7	21.9	0.5	12.1	16.9	42.5
600–650nm		23.1	18.1	9.4	26.1	39.2	32.8
650–700nm		31.1	21.1	36.1	35.0	21.0	9.5
700–750nm		14.1	1.6	0.0	16.4	5.4	4.1
750–800nm		3.8	0.5	0.0	4.3	1.2	3.7
Pr:Ptotal		0.747	0.826	0.825	0.750	0.812	0.819
CRY2 eff.		0.198	0.304	0.426	0.099	0.217	0.224
R:FR		2.733	30.300	NA	2.575	6.501	3.149
B:G		1.114	0.751	169.961	0.011	1.846	0.230
B:PAR		0.136	0.194	0.531	0.001	0.134	0.035
G:PAR		0.122	0.259	0.003	0.128	0.072	0.150
R:PAR		0.161	0.161	0.303	0.181	0.120	0.019

The six spectra were chosen for the experiment because of their divergent characteristics, all treatments had a wide spectrum covering different wavelengths of the visible spectrum (390-700nm). Specifically, the effect of blue wavebands was examined with the AP67 and AP67 accompanied with a blue-light excluding filter (AP67B). AP67B was implemented by placing a Rosco #312 yellow coloured plastic filter (Rosco-filters: Westlighting, Helsinki, Finland) under AP67 LED luminaires, so removing blue light from the spectrum (Figure 3). The effects of green wavebands was studied with the AP3 treatment, which had 16.5 % of its photons between 500 and 550 nm; in comparison, treatment AP9 contained only 0.2 % green photons in its spectrum. The effect of R:FR ratio on growth and morphology was examined with all spectra; R:FR photon ratio varied from 2.6 to 30.3 between spectra, furthermore, AP9 emitted no radiation between 700 and 800 nm. The effect of small differences in R:FR and B:G ratios could be examined by comparing the growth in treatments AP67 and AP673L.

Figure 3 Treatment AP67B: AP67 LED bars covered with a yellow plastic filter to remove blue light from the original spectrum. Photo: Titta Kotilainen.

8.3 Water deficit treatment

Moisture content of the rock wool cube was monitored weekly with a water content meter, Grodan® (Roermond, Netherlands). Water content was maintained between 50 and 85 %v/v in all cubes before the water deficit treatment commenced. The water deficit treated cubes were marked beforehand on the first week of the experiment with yellow nametags. The water stress treatment started 30 days after sowing, on February 19th, when irrigation was limited until the water content in the cubes declined below 30% v/v, where it was maintained for three days. During the water deficit period, moisture content measurements were conducted daily. When water content in the cube declined below 20 v/v%, nutrition solution was added by hand to reach the desirable level (20–30 v/v%) in order to avoid excess wilting. Water content was measured from four cubes in each experimental plot; two normally irrigated cubes and two drought treated cubes. The water content of the rock wool cubes during the experiment is presented in Table 4.

Table 4 Water content of the rock wool cubes (v/v%) prior to and during water stress treatment in light treatments AP67, AP3, AP9, AP67B, AP673L, and HPS. Values are means of four measurements per light treatment. Wet = measurements from normally irrigated cubes, Dry = measurements from drought treated cubes.

| | Measurement date | | | | | | | | |
| | 29.1. | 4.2. | 11.2. | 19.2. | | 21.2. | | 22.2. | |
Treatment	Wet	Wet	Wet	Wet	Dry	Wet	Dry	Wet	Dry
AP67	79	80	79	64	60	70	23	58	17
AP3	77	85	76	67	70	64	19	55	22
AP9	82	79	77	72	75	72	31	73	24
AP67B	82	84	77	63	63	68	26	71	23
AP673L	78	84	74	61	66	50	31	59	19
HPS	83	86	76	60	55	62	23	57	24

8.4 Measurements of vegetative growth

Vegetative growth of eight plants, four water-stressed and four normally irrigated, from each compartment was measured in the end of the experiment. From each of the eight plants, the plant vertical height from the cube surface, stem diameter at 1 cm from the cube surface, leaf number, leaf area, and total fresh weight of the shoots were measured. The leaf area was measured with LI-3000C scanning head (Lincoln, Nebraska, USA) attached to a transparent belt conveyor accessory (LI-3050C, Lincoln, Nebraska, USA). The leaf midrib was excluded from leaf area measurements. The individual leaf size was evaluated by measuring the leaf petiole length and the leaf blade length of one fully matured leaf of each plant.

After the fresh weight measurements, the shoots were placed into paper bags and dried in an oven (70 $^{\circ}$C) for 48 hours to a constant weight before dry weight measurements.

8.5 Generative growth

Generative growth was measured at the end of the experiment from 16 plants from each treatment by counting the number of buds. The number of buds indicates the potential yield formation. The generative growth stage of a tomato plant can be evaluated by the number of opened flowers or total number of buds. In this experiment no flowers were open by the end of the study. Therefore the average number of buds was used as a developmental stage indicator. Buds larger than 3mm in length were counted.

8.6 Stomatal conductance and photosynthesis

From each plant, a leaflet from a fully expanded leaf was marked with a wire ring beforehand for leaf temperature measurements. The leaf temperature was measured from the same leaflet twice during the experiment; prior to the water deficit treatment to compare the leaf temperature differences between light treatments, and during the water deficit treatment to test the effect of drought on leaf temperature under different light quality treatments.

8.6.1 Leaf temperature measurements

Stomatal conductance was studied by measuring the leaf temperature with a laser IR thermometer (Optris lasersight LS LT, Berlin, Germany) twice during the experiment. The first measurement was performed before the water deficit treatment and the second during the drought treatment. On both measurement dates, the measurements were conducted on each plant in each compartment; 32 measurements per treatment.

In addition to the laser sight leaf temperature measurements, the plants were photographed with a thermal camera (Optris PI450 thermal imager, Optris GmbH, Berlin, Germany) during the water deficit period to compare leaf temperature differences between light treatments and drought treatments. From each compartment two normally irrigated and two water stressed plants were photographed; altogether eight plants per

light treatment. In the thermal photograph, a wet tissue paper watered with RO-water and a dry tissue paper, were placed next to the photographed plants to create a temperature-evaporation scale. The wet tissue paper represented the extreme low leaf temperature and the dry tissue paper represented the highest possible dry leaf temperature. From the extreme temperatures and measured leaf temperatures, a crop water-stress index (CWSI,) was calculated according to Grant et al. 2006 (Equation 1). CWSI value is between 0 and 1, the closer the value is to 0, the 'drier' the plant is, in other words the smaller the cooling my transpiration is.

$$(T\text{dry} \; - T\text{leaf}) \quad / \quad (T\text{dry} - T\text{wet}) \quad = \text{CWSI} \tag{1}$$

In which,

Tdry = temperature of the dry tissue paper

Tleaf = measured leaf temperature

Twet = temperature of the watered tissue paper

CWSI = Crop Water Stress Index

8.6.2 Leaf level gas exchange

Unshaded fully-expanded leaves from the upper 3rd of the plant were selected and their photosynthesis, stomatal conductance, and ratio of intra-cellular to ambient CO_2 concentration (Ci/Ca), were recorded. These photosynthesis and stomatal conductance readings were normalized to the same PAR dose to account for differences in the PAR received under each treatment and at different distances from the lamp. Two measurements of gas exchange were registered; the first, "initial", on reaching a temporary stable state, usually attained within a minute of positioning the leaf inside the LICOR6400 chamber and reflecting the actual performance of the leaf in the ambient conditions in each compartment at the time of sampling; the second measurement, "stable", was registered once gas exchange parameters had fully-acclimated to the stable conditions of temperature (23°C), CO_2 (400 ppm) and VPD (1.5–1.8 KPa) in the LICOR6400 leaf chamber after 5–10 minutes and was reflective of a more standardized,

though similar, environment than that which occurred in the greenhouse during the period of measurement. Stable measurements were used in the statistical analysis.

8.7   Leaf chlorophyll, flavonoid, and abscisic acid content

The leaf chlorophyll content was measured *in vivo* twice from all plants. The measured leaves were marked in advance with a wire ring. Leaf chlorophyll was measured with SPAD 502 (Konica Minolta, Osaka, Japan), which measures the total leaf chlorophyll in SPAD units. The first measurement day was prior to the water deficit treatment, on February 19th, when all plants in each treatment were measured; a total of 32 measurements per treatment. By measuring all plants before the water deficit treatment, the effect of light quality on chlorophyll content could be evaluated. The second measurement day was during the water deficit treatment, on the 21st of February, when 16 water stressed plants (marked in advance) from each treatment were measured. The effect of water deficit on chlorophyll content could be evaluated because measurements were conducted prior to and during the water deficit period from the same leaves.

The phenolic content of the epidermis was estimated twice from all plants with a flavonoid content meter (Dualex 3.3 Force-A, Houston, Texas, USA). The measured leaflets were marked in advance with a wire ring. The flavonoid content was first measured prior to the water deficit treatment, on February 19th, from all plants; and again two days later, on February 21st, from 16 water stressed plants (marked in advance) from each light treatment. By measuring the flavonoid content before and during the water deficit treatment, the effect of the drought stress on the phenolic content of the tomato leaves in different light conditions could be studied.

From four wet and water stressed plants, a leaflet, at the tip of the tomato leaf, (Figure 4) was cut and sampled for hormone content analysis. A fully-expanded leaf from the upper 3rd of the plant was selected for ABA content analysis. Together the four leaflets collected from each light compartment were pooled for one sample. Leaflets were placed in aluminum foil and in liquid nitrogen, and transferred into a freezer (-71 °C) for later analysis.

From the frozen tomato leaf pieces, a small piece (~1 mg) was first weighed fresh and then dry with analytical balance (Scaltec instruments GmbH, Heiligenstadt, Germany), in order to calculate the dry matter content of the samples. The remaining leaf matter was ground in liquid nitrogen with mortar and pestle. From each sample, three parallel sub-samples were prepared. 120 mg of ground leaf mass was extracted with 600 µl methanol (MeOH/isopropanol 20:80, 1% acetic acid) and standards: 2 µl of D_6ABA (100 ng/µl in MeOH) and 2µl of D_5IAA (1 µl/1ml). Samples were shaken at +4°C for 30 minutes after which they were centrifuged for 10 minutes at 13 000 rpm in +4 °C. Supernatant was collected in a clean eppendorf tube and the pellet was extracted with 600 µl methanol (MeOH/isopropanol 20:80, 1% acetic acid), shaking and centrifuging was repeated. Supernatants were combined and liquid was vapourised with –OH in +50°C for 60 minutes with a Genevac miVac Duo concentrator (Ipswich, United Kingdom). Dried sample was extracted into 200 µl of MeOH, which was analyzed with an ultra-performance liquid chromatography system (Acquity UPLC ®,Waters, MA, USA) . The absorbance area of ABA was divided by the sample fresh weight and normalized to the absorbance area of the standard D_6ABA. The normalized ABA content was then multiplied by the total added standard mass (200 ng) and the dry matter content of the weighed leaf sample.
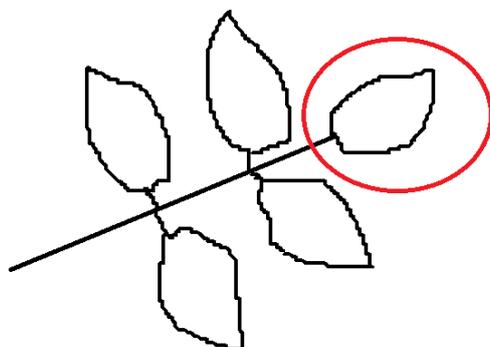
Figure 4 A tomato leaf, from which the sample for hormone analysis was taken from the top leaflet, circled in red.

8.8 Statistical analysis

Data were analysed with the R system for Statistics (ver 3.0.1) running under RStudio. The effect of treatment was tested with Linear mixed effect model (LME) (R package nlme, Pinheiro and Bates, 2013) when residuals revealed heterogeneity of variance, a

power variance covariate was included in the fitted model argument "weights=varPower" of function lme. In the model used in the statistical analysis, the data were described as nested so that the analysis of variance was run using the compartment mean values.

When light quality effects on growth and photosynthesis were tested with one-way-ANOVA, only the data collected from normally irrigated plants was used. When testing the effect of light treatment and drought together with a two-way-ANOVA, the data contained both normally irrigated and water stressed values. A three-way- ANOVA was used to test the effect of light treatment, drought, and measuring time (day) on leaf temperature, total chlorophyll and flavonoid contents.

Correlations were tested with the R System for Statistics (version 3.0.1), by using the command "cor.test". Data collected from normally irrigated plants and drought treated plants were tested separately.

9 RESULTS

Results section is divided into results about the light quality effects on the morphological traits of tomato plants, and results about the drought tolerance and stomatal conductance of seedlings under different light treatments during drought.

9.1 Light quality effects on growth and morphology

Vegetative growth was measured at the end of the experiment. Measurements included plant height, stem diameter, shoot fresh weight and dry weight. The number of leaves was counted and the total leaf area was measured. All measurements were recorded from the water deficit treated and normally irrigated plants separately.

9.1.1 Stem height and internode length

Plants grew tallest under the AP67B lamps, where plants were 53.2 cm high on average (Table 5). The shortest plants were under the AP9 lamps, where the average plant height

was 21.4 cm. The height difference was small between treatments AP67, AP67B and HPS was small (Figure 5). Internodes were likewise longest in treatments AP67 and HPS and shortest in treatment AP9. Differences in plant height and internode length were statistically significant.

Table 5 Plant height (cm), and internode length (cm) of the tomato plants at the end of the experiment. Values are means ± 1 SE of 8 plants per treatment; the measured plants were irrigated normally throughout the experiment.

Treatment	Plant height (cm)	Internode length (cm)
AP67	50.6 ±4.4	5.1 ±1.0
AP3	37.2 ±4.5	4.3 ±0.8
AP9	21.4 ±3.0	2.8 ±0.4
AP67B	53.2 ±4.5	4.9 ±0.3
AP673L	42.0 ±6.1	4.1 ±0.6
HPS	52.2 ±6.2	5.1 ±0.8
Statistics		
Treatment	$F_{5,6} = 26.9$ $P < 0.001$	$F_{5,6} = 8.2$ $P = 0.0116$

Figure 5 Normally irrigated tomato plants prior to drought treatment. From left to right: AP9, AP3, AP673L, AP67, HPS, AP67B. Photo: Titta Kotilainen.

9.1.2 Fresh weight, dry weight and dry matter content

Plants grown under the HPS had the highest shoot fresh weight (67.3 g) and dry weight (5.9 g). However, the highest dry matter content was measured from treatments AP673L and AP9, in which the dry matter content was 8.8 %. Fresh weight and dry weight differences between treatments were statistically significant (Table 6)

Table 6 Fresh and dry weight (g), and dry matter content (%) of the tomato shoots at the end of the experiment. Values are means ± 1 SE of 8 plants per treatment; the measured plants were irrigated normally throughout the experiment.

Treatment	Fresh weight (g)	Dry weight (g)	Dry matter content (%)
AP67	63.5 ±11.2	5.0 ±0.9	7.9 ±0.5
AP3	48.8 ±9.8	3.8 ±0.7	7.9 ±0.8
AP9	26.5 ±5.1	2.3 ±0.4	8.8 ±0.2
AP67B	66.1 ±12.3	5.1 ±0.9	7.8 ±0.6
AP673L	65.7 ±14.5	5.8 ±1.5	8.8 ±0.9
HPS	67.3 ±10.6	5.9 ±0.9	8.7 ±0.4
Statistics			
Treatment	$F_{5,6} = 34.61$	$F_{5,6} = 6.82$	$F_{5,6} = 3.97$
	$\boldsymbol{P < 0.000}$	$\boldsymbol{P = 0.018}$	$P = 0.062$

9.1.3 Number of leaves, leaf area and leaf size

The highest number of leaves per plant on average was in treatment AP67B, in which the average leaf number was 11; the lowest number of leaves on average was in treatment AP9 with a mean of 8 leaves per plant. The difference in leaf number between light treatments was statistically significant (Table 7). The largest individual leaves were measured in treatment AP67B, where the petiole was 8.1 cm and the leaf blade 35.0 cm long on average. The smallest measured leaves were in treatment AP9, the petiole was 6.4 cm and the leaf blade 24.6 cm long in average. Differences in petiole length between light treatments were evident (Figure 6). Largest total leaf area per plant was measured from treatment AP67B, in which its average was 1561.0 cm^2; while the average was in treatment AP9 (724.3 cm^2) (Table 7).

Table 7 Number of leaves, total leaf area, leaf blade length, and petiole length of the normally irrigated plants in the end of the experiment in treatments AP67, AP3, AP9, AP67B, AP673L and HPS. Values are means ±1 SE of eight measured plants per treatment.

Treatment	Number of leaves		Leaf area (cm^2)		Leaf blade length (cm)		Petiole length (cm)	
AP67	10	±1	1376.3	±178.6	34.4	±2.4	8.0	±0.8
AP3	9	±1	1117.1	±229.3	31.8	±3.4	7.8	±0.7
AP9	8	±0	724.3	±115.6	24.6	±2.4	6.4	±0.7
AP67B	11	±1	1561.0	±245.0	35.0	±1.5	8.1	±0.7
AP673L	10	±1	1313.8	±207.5	31.4	±2.2	7.2	±0.9
HPS	10	±1	1269.6	±142.2	33.6	±1.3	7.1	±0.8
Statistics								
Treatment	$F_{5,6} = 9.0$		$F_{5,6} = 17.0$		$F_{5,6} = 37.6$		$F_{5,6} = 4.4$	
	$P = 0.009$		$P = 0.002$		$P < 0.001$		$P = 0.049$	
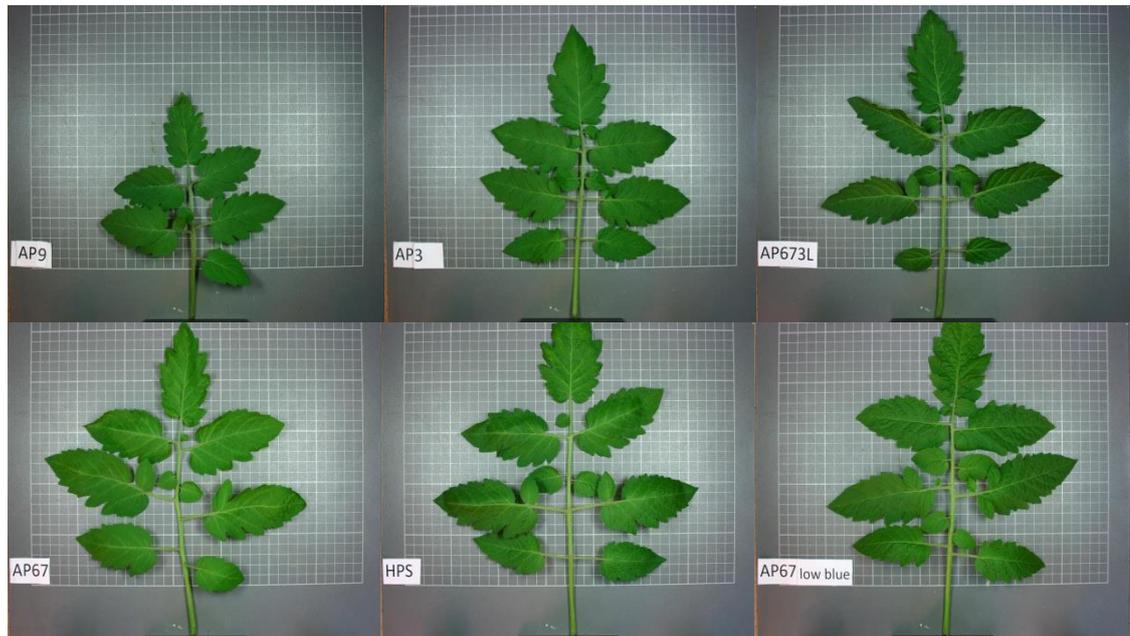
Figure 6 The petiole length of tomato plants differed when grown under six different light quality treatments. Lines in the grating are 1 cm apart.

Shoot fresh weight, plant height, and petiole length correlated negatively with blue and violet waveband irradiance (Table 8), correlation between shoot fresh weight, plant height and red waveband irradiance was also negative. The green waveband irradiance positively correlated with petiole length; the higher the green light fraction given in a spectrum, the

longer the petiole length. Green light, did not however, correlate with fresh weight or shoot height, but yellow and orange had strong positive correlations with these two growth parameters. The strong positive correlation between fresh weight, plant height, petiole length, and FR irradiance was as expected, as well as the negative correlation between R:FR, fresh weight and plant height.

Table 8 Correlations between percent contribution of different wavebands to total photon irradiance, R:FR photon irradiance ratio, B:G photon irradiance ratio, Pr:Ptotal ratio, CRY2 effective photon irradiance, and growth parameters (fresh weight, plant height, and leaf petiole length). Values are from normally irrigated plants only. The degrees of freedom for R:FR and fresh weight, plant height, and petiole length is 38. Significance level: **P<0.05**, ****P<0.01**, ****P<0.001**. See Table 3 for light related mean values, and Tables 5, 6, and 7 for growth related mean values.

	Fresh weight Df = 46 or 38	Plant height Df = 46 or 38	Petiole length Df = 46 or 38
Violet	-0.79***	-0.90***	-0.45**
Blue	-0.78***	-0.87***	-0.49***
Green	0.06	0.09	0.39**
Yellow	0.45**	0.48***	0.04
Orange	0.70***	0.618***	0.14
Red	-0.36*	-0.30*	0.06
FR 700-750 nm	0.51***	0.68***	0.48***
FR 750-800 nm	0.62***	0.84***	0.38**
R:FR	-0.51***	-0.67***	0.04
B:G	-0.74***	-0.79***	-0.49***
Pr:Ptotal	-0.40**	-0.58***	-0.46***
CRY2:light	-0.74***	-0.85***	-0.49***

9.1.4 Generative growth

Generative growth was measured at the end of the experiment by counting the buds on eight normally irrigated plants from each treatment. The mean number of buds in each treatment is presented in Table 9. Highest number of buds on average was in plants from treatment AP67, in which the mean bud number was 9.1; the lowest mean bud number was in treatment AP9, in which each plant had 2.3 buds on average. Differences in the mean bud number between light treatments were statistically significant.

Table 9 The total number of buds in treatments AP67, AP3, AP9, AP67B, AP673L, and HPS, the values are means from 8 plants per treatment ±1 SE.

Treatment	Number of flower buds
AP67	9.1 ±4.0
AP3	4.9 ±2.4
AP9	2.3 ±1.7
AP67B	8.6 ±3.0
AP673L	7.6 ±3.0
HPS	7.3 ±2.9
Statistics	
Treatment	$F_{5,6} =12.1$ ***P* = 0.004**

9.2 Light quality effects on stomatal conduction and photosynthesis

Light quality effects on gas exchange were studied by measuring the leaf temperature, photosynthesis and stomatal conductance of the normally irrigated plants. The CWSI was also calculated from the normally irrigated plants, in order to see, whether the light quality affected the CWSI under normal growth conditions.

9.2.1 Leaf temperature, photosynthesis, stomatal conductance, and CWSI

Table 10 presents the average values for leaf temperature, photosynthesis, stomatal conductance and CWSI for the six light treatments. The highest leaf temperature in normally irrigated plants was measured from treatment HPS, and lowest in treatment AP9, differences in the leaf temperature between light treatments were statistically significant (Table 10). The average photosynthetic rate was highest in treatment AP67, and lowest in treatment HPS. Stomatal conductance prior to the water deficit treatment was lowest in AP9 and highest in AP673L. CWSI indicates the water stress level of the plants; the closer the value is to 0, the more stressed the plant is. The highest CWSI was calculated in treatment AP9 and lowest in treatments AP67B and AP673L.

Table 10 Effect of light quality on leaf temperature, stomatal conductance, photosynthesis and crop water stress index (CWSI). The leaf temperature of all plants in each treatment was measured; the value is the mean of 32 measurements ± 1 SE. Conductance, photosynthesis, and CWSI were measured in 4 plants per treatment; the value is the mean of 4 measurements ± 1 SE. All values are for normally irrigated plants. Stable values of photosynthesis and stomatal conductance are divided by the PAR received, in order to correct the values for the differences in PAR irradiance received by the different leaves.

Treatment	Leaf °C		Photosynthesis		Conductance		CWSI	
	19.2.2013		μmol CO_2 m^{-2} s^{-1}		mol H_2O m^{-2} s^{-1}			
AP67	20.43	± 0.030	30.3	± 1.8	0.324	± 0.10	0.50	± 0.22
AP3	19.79	± 0.027	26.8	± 7.5	0.195	± 0.43	0.36	± 0.07
AP9	18.80	± 0.025	25.2	± 1.4	0.231	± 0.08	0.56	± 0.07
AP67_B	19.89	± 0.022	25.7	± 3.1	0.261	± 0.01	0.31	± 0.12
AP673L	19.77	± 0.025	25.3	± 8.1	0.514	± 0.24	0.31	± 0.10
HPS	21.46	± 0.023	22.6	± 4.2	0.488	± 0.14	0.41	± 0.09
Statistics								
Treatment	$F_{5,6} = 25.82$		$F_{5,6} = 2.44$		$F_{5,6} = 0.98$		$F_{5,6} = 3.57$	
	P < 0.001		*P = 0.077*		*P = 0.459*		***P = 0.023***	

Prior to drought, leaf temperature was measured from all plants in each compartment with an infrared thermometer. The leaf temperature negatively correlated with short waveband violet and blue as well as red irradiation. Yellow and orange wavebands strongly positively correlated with leaf temperature; the higher the yellow and orange waveband fraction in a spectrum, the higher the leaf temperature. Photosynthesis and conductance did not have statistically significant correlations with the proportion of photon irradiance in the different wavebands. CWSI was calculated from the normally irrigated plants to test possible waveband correlation with the water stress index value. Violet and blue wavebands and CRY2 effective photon irradiance ratio correlated positively with CWSI, whereas yellow wavebands, orange wavebands, and FR between 750 and 800 nm correlated negatively (Table 11).

Table 11 Correlations between percent contribution of different wavebands to total photon irradiance, R:FR photon irradiance ratio, B:G photon irradiance ratio, Pr:Ptotal ratio, CRY2 effective photon irradiance, and conductance parameters (leaf temperature ºC, photosynthesis, conductance, and CWSI). Stable values of photosynthesis and stomatal conductance were divided by the PAR received, in order to correct for differences in the received PAR. Values are from normally irrigated plants only. Degrees of freedom for R:FR and leaf temperature is 78, and for photosynthesis, conductance and CWSI 17. Significance level: *** P<0.05, ***P<0.01, **P<0.001***.

	Leaf temperature Df = 94 or 78	Photosynthesis Df = 21 or 17	Conductance Df = 21 or 17	CWSI Df = 21 or 17
Violet	**-0.41***	0.14	-0.11	**0.48***
Blue	**-0.34***	0.14	-0.16	**0.54***
Green	0.03	0.18	0.21	-0.15
Yellow	**0.50***	-0.16	-0.02	**-0.41***
Orange	**0.30***	-0.13	0.00	**-0.45***
Red	**-0.44***	0.07	0.07	0.37
FR 700–750 nm	0.11	-0.05	0.12	-0.31
FR 750–800 nm	**0.38***	-0.16	0.04	**-0.44***
R:FR	-0.15	0.17	0.13	0.18
B:G	**-0.38***	0.12	-0.14	**0.58***
Pr:Ptotal	-0.13	-0.02	-0.09	0.25
CRY2:light	**-0.42***	0.16	-0.15	**0.46***

9.2.2 Leaf total chlorophyll content

The total chlorophyll content of the leaves was measured prior to the water deficit treatment (19.2.2013) in order to examine the light quality effects on chlorophyll content. Chlorophyll content was highest in treatment AP673L, where the average SPAD value was 48.7, and lowest in treatment AP67B (42.2) (Table 12).

9.2.3 Total flavonoid content in the upper epidermis

The flavonoid content was measured from all plants on February 19th; a total of 32 measurements per treatment. The results are presented in (Table 12). The highest flavonoid content was in treatment AP673L and the lowest in AP67B, 0.38 and 0.12

absorption units, respectively. The differences in total flavonoid content measured from the leaf upper epidermis were statistically significant (Table 12).

9.2.4 Leaf ABA content

The results from the ABA extraction are presented in Table 12. Among the normally irrigated plants, the ABA content was highest in treatment HPS (231 ng/g) and lowest in treatment AP3 (88 ng/g).

Table 12 Flavonoid content, SPAD chlorophyll value, and the ABA content of the normally irrigated plants. The flavonoid and SPAD values are means from 16 measurements per treatment given in absorption units ±1SE. Mean ABA content is calculated from two median values per treatment ±1SE, median was calculated from three values per replicate.

Treatment	Flavonoid content	SPAD-value	ABA content ng/g
AP67	0.20 ±0.1	43.6 ±3.1	125.4 ±80.6
AP3	0.22 ±0.1	43.6 ±3.7	88.1 ±32.8
AP9	0.31 ±0.1	45.9 ±3.1	92.9 ±48.6
AP67B	0.12 ±0.1	42.2 ±2.8	154.4 ±88.3
AP673L	0.38 ±0.2	48.6 ±2.5	189.0 ±42.4
HPS	0.19 ±0.1	47.8 ±4.1	231.3 ±195.5
Statistics			
Treatment	$F_{5,6} = 18.16$	$F_{5,6} = 16.09$	$F_{5,6} = 1.49$
	$P = 0.001$	$P = 0.002$	$P = 0.3167$

9.2.5 Correlations between light quality and leaf chlorophyll and flavonoid content

The total flavonoid content in the leaf upper epidermis positively correlated with short wavelength violet and blue irradiance, whereas green, yellow, far-red 700–750 nm, and far-red 750–800 nm negatively correlated with total flavonoid content (Table 13). The leaf chlorophyll content positively correlated with yellow and orange wavelength irradiation, and negatively with red and far-red irradiation. High Pr:Ptotal ratio and CRY2 effective photon irradiance positively correlated with leaf upper epidermis total flavonoid and leaf total chlorophyll contents.

Table 13 Correlations between percent contribution of different wavebands to total photon irradiance, R:FR photon irradiance ratio, B:G photon irradiance ratio, Pr:Ptotal ratio, CRY2 effective photon irradiance, and leaf upper epidermis flavonoid and total chlorophyll contents. Values are from normally irrigated plants only. Degrees of freedom in R:FR and flavonoids is 155 and SPAD-value 151. Significance level: *** $P<0.05$, **$P<0.01$, ***$P<0.001$.**

	Flavonoids Df = 187 or 155	SPAD-value Df = 183 or 151
Violet	**0.34*****	0.09
Blue	**0.34*****	0.13
Green	**-0.20****	-0.08
Yellow	**-0.17***	**0.27****
Orange	0.08	**0.20****
Red	-0.04	**-0.40*****
FR 700–750 nm	**-0.37*****	**-0.43*****
FR 750–800 nm	**-0.47*****	**-0.29*****
R:FR	0.06	0.14
B:G	**0.25****	0.03
Pr:Ptotal	**0.36*****	**0.47*****
CRY2:light	**0.34*****	**0.23****

9.3 The effect of water deficit on growth parameters under different light quality

The water deficit treatment was applied towards the end of the experiment, when water supply was limited over three days for half of the plants. The effect of water deficit on growth was recorded by measuring plant fresh and dry weight, leaf number, leaf area, plant height, and shoot diameter.

9.3.1 Plant height and internode length

In all light treatments, the average plant height was lower in water stressed plants than in the normally irrigated plants (Table 14), the drought effect on plant height was statistically significant (P = 0.002). However, the interaction between drought and light treatments was not statistically significant. Plant height in treatment AP3 was least affected by drought (5 % decrease), whereas in treatments AP673L and HPS the plant height of the water stressed plants was 14 % and 12 % shorter, respectively.

Table 14 Effect of water deficit on tomato stem diameter and plant height growth. Mean values are averages of 8 plants per treatment ±SE.

Treatment	Plant height (cm)			Internode length (cm)		
	Wet	Dry	Diff %	Wet	Dry	Diff %
AP67	50.6 ±4.4	46.7 ±7.2	-8	5.1 ±1.0	5.3 ±1.0	4
AP3	37.2 ±4.5	35.4 ±2.8	-5	4.3 ±0.8	4.2 ±0.7	-3
AP9	21.4 ±3.0	19.6 ±2.4	-8	2.8 ±0.4	2.4 ±0.4	-12
AP67_B	53.2 ±4.5	48.5 ±3.9	-9	4.9 ±0.3	5.2 ±0.6	4
AP673L	42.0 ±6.1	36.0 ±4.8	-14	4.1 ±0.6	3.7 ±0.6	-10
HPS	52.2 ±6.2	45.9 ±6.3	-12	5.1 ±0.8	5.7 ±1.1	11
Statistics						
Treatment	$F_{5,6} = 39.8$		**P = 0.0002**	$F_{5,6} = 21.7$		**P = 0.0009**
Drought	$F_{1,6} = 28.4$		**P = 0.0018**	$F_{1,6} = 9.7$		**P = 0.0209**
Interaction	$F_{5,6} = 1.1$		P = 0.4409	$F_{5,6} = 2.1$		P = 0.1953

9.3.2 Fresh weight and dry weight

Shoot fresh weight of the water stressed plants was lower than the shoot fresh weight of the normally irrigated plants. In treatment HPS, the mean fresh weight of the water-stressed plants was 24 % smaller than the fresh weight of the normally irrigated plants, whereas in treatment AP3 the equivalent decrease was only 3 %. Water deficit affected fresh weight significantly (P = 0.001), however the interaction between drought and light treatments was not quite statistically significant (P = 0.0685). As with fresh weight, the dry weight decreased in all light treatments due to water stress. In treatment HPS, the dry weight of the water stressed plants was 29 % lower than the dry weight of the normally irrigated plants. The drought impact on dry weight was statistically significant (P = 0.007), but again, the interaction between drought and light treatments was not statistically significant (P= 0.1297) (Table 15).

Table 15 Effect of water deficit on tomato fresh and dry weight. Mean values are averages of 8 plants per treatment ±1 SE. The difference between the wet and dry plants is presented in percentages (Diff.).

Treatment	Fresh weight (g)					Dry weight (g)				
	Wet		Dry		Diff %	Wet		Dry		Diff %
AP67	63.5	±11.2	48.2	±7.86	-19	5.0	±0.9	4.1	±0.9	-17
AP3	48.8	±9.8	45.4	±10.4	-3	3.8	±0.7	3.7	±0.6	-3
AP9	26.5	±5.1	22.0	±3.5	-9	2.3	±0.4	2.0	±0.4	-12
AP67_B	66.1	±12.3	47.2	±6.3	-20	5.1	±0.9	3.8	±0.6	-26
AP673L	65.7	±14.5	46.9	±9.7	-18	5.8	±1.5	4.4	±1.0	-25
HPS	67.3	±10.6	45.2	±11.8	-24	5.9	±0.9	4.2	±1.0	-29
Statistics										
Treatment	$F_{5,6} = 92.8$ ***P < 0.001***					$F_{5,6} = 71.6$		***P < 0.001***		
Drought	$F_{1,6} = 35.2$ ***P = 0.001***					$F_{1,6} = 16.4$		***P = 0.007***		
Interaction	$F_{5,6} = 3.8$ $P = 0.069$					$F_{5,6} = 2.7$		$P = 0.129$		

9.3.3 Number of leaves and leaf area

The number of leaves of the water stressed plants was lower in all light treatments, except in treatment AP9. In addition to the differences in total leaf number, also the leaf area of the water stressed plants was lower on average than the leaf area of the normally irrigated plants. The largest (31 %) difference in the leaf area between normally irrigated and water stressed plants was recorded in treatment HPS, and the lowest in treatments AP3 and AP9, in which the difference was 13 % (Table 16).

Table 16 Water stress effect on number of leaves and total leaf area of tomato. Mean values are calculated from eight plants per treatment ±1 SE, difference between wet and dry plants mean values is presented in percentages (Diff.).

Treatment	Number of leaves			Leaf area (cm^2)		
	Wet	Dry	Diff. %	Wet	Dry	Diff. %
AP67	10 ±1	9 ±1	-11	1117 ±178	1091 ±124	-21
AP3	9 ±1	9 ±1	-3	1376 ±229	975 ±129	-13
AP9	8 ±0	8 ±1	5	1561 ±115	631 ±87	-13
AP67_B	11 ±1	9 ±1	-12	1313 ±244	1152 ±155	-26
AP673L	10 ±1	10 ±1	-4	1724 ±207	1026 ±198	-22
HPS	10 ±1	8 ±1	-20	1269 ±142	875 ±214	-31
Statistics						
Treatment	$F_{5,6} = 9.84$ *P= 0.007*			$F_{5,6} = 17.80$ *P = 0.002*		
Drought	$F_{5,6} =12.56$ *P= 0.012*			$F_{5,6} = 58.82$ *P < 0.001*		
Treatment:Drought	$F_{5,6} = 2.54$ *P= 0.144*			$F_{5,6} = 2.26$ *P = 0.175*		

The water deficit treatment did not affect bud number in treatments AP3, AP9, and HPS, but lowered the average bud number in treatments AP67, AP67B, and AP673L, results were not however statistically significant.

9.4 The effect of water deficit on stomatal conductance and photosynthesis in different light quality

Leaf temperature, stomatal conductance, photosynthesis, and Ci/Ca were measured to study the effect of water stress on stomatal conductance under varying light quality. Gas exchange parameters were used to evaluate the stress level plants were experiencing under different light spectra.

9.4.1 Leaf temperature

The leaf temperature was measured prior to, and during the water deficit treatment. Leaf temperature was measured from the same leaf at both measuring times to demonstrate the effect of drought stress on stomatal closure. When measured prior to water stress, the leaf temperature was highest in the HPS treatment and lowest in AP9 treatment, where the average leaf temperatures were 21.46 °C and 18.81 °C, respectively. The water deficit treatment increased the leaf temperature in all treatments, in all compartments (Figure 7). AP67 and AP67B had the lowest increase in the leaf temperature (3%), whereas in treatment AP3 the average leaf temperature increased 10 % during the water deficit treatment. Leaf temperature of the normally irrigated plants generally increased between measurement days, except in treatments AP67 and AP67B (Figure 8). The effect of measurement day on leaf temperature was not statistically significant. Stomatal closure by tomato plants during water stress under AP3 spectrum is illustrated by the thermal camera image (Figure 9).
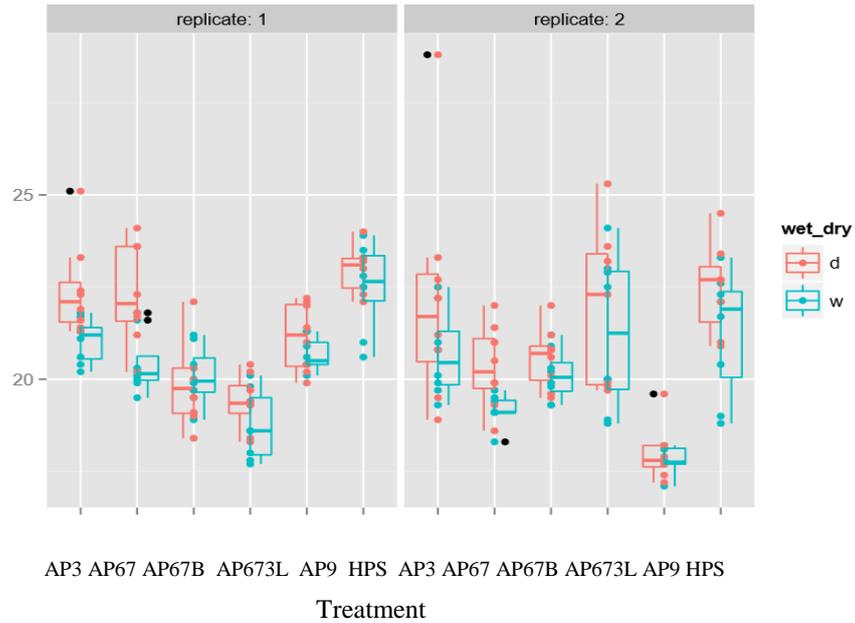
Figure 7 The leaf temperature measured during water deficit from all compartments; replicate one and replicate two of light treatments AP3, AP67, AP67B, AP673L, AP9, and HPS. The red boxplots are measurements from eight drought stressed plants, blue boxplots from eight normally irrigated plants.
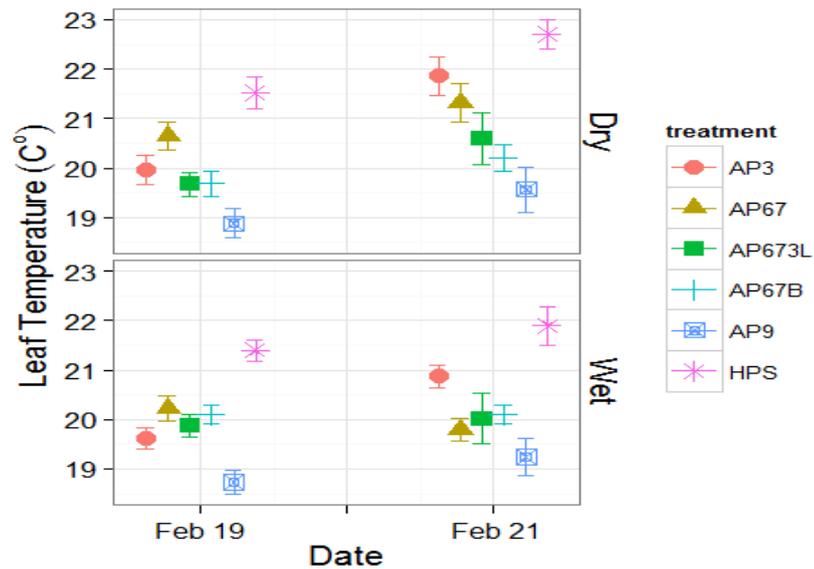
Figure 8 Leaf temperature in light treatments AP3, AP67, AP673L, AP67B, AP9, and HPS in normally irrigated plants and water stress treated plants prior to (Feb 19) and during (Feb 21) water stress treatment. The effect of drought treatment on leaf temperature was statistically significant (**P < 0.001**). The interaction effect of light treatment and drought was statistically significant (**P = 0.041**). The effect of measurement day was not statistically significant (P = 0.0829). The interaction effect of drought and date was significant (**P = 0.003**), however the interaction effect of light treatment and date was not.
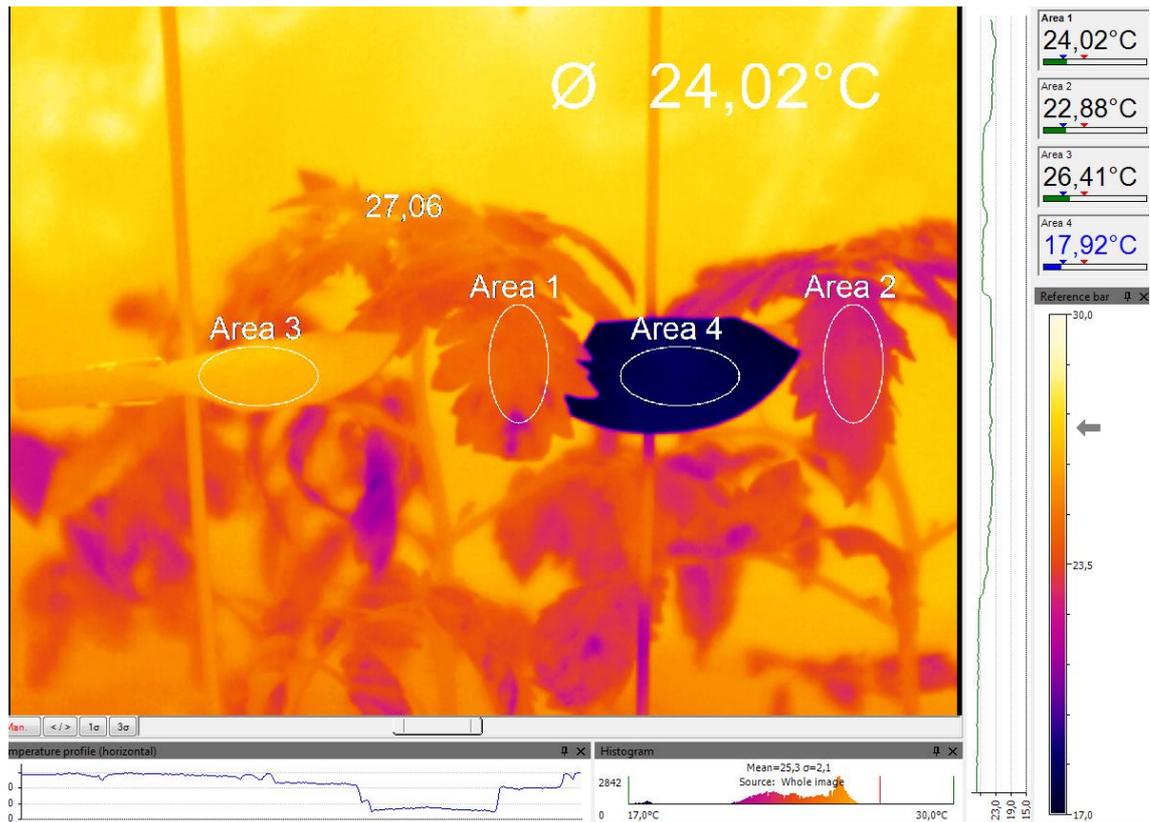
Figure 9 A Thermal camera image of a water stressed tomato plant (area 1) and a normally irrigated plant (area 2) under treatment AP3. Area 3 is a dry tissue paper, representing the highest possible leaf temperature value in the compartment. Area 4 is a wet saturated tissue paper, representing the lowest possible leaf temperature value in the compartment. The mean temperature of each area is reported in the upper right corner of the image. Picture was taken on 20th of February. Photo: Titta Kotilainen and Stiina Kotiranta.

9.4.2 Photosynthesis, stomatal conductance, and Ci/Ca ratio

Stomatal conductance was lower in the water stressed plants than in the normally irrigated plants under all light treatments. The largest difference in stomatal conductance between dry and wet plants was measured in light treatments AP67B and AP3, in which the difference was 55%. Treatment AP673L had the smallest difference in conductance between normally irrigated and water stressed plants. The ratio between intracellular CO_2 and CO_2 in the atmosphere (Ci/Ca) was lowest in AP67 in the normally irrigated plants, however the Ci/Ca ratio was highest in the water stressed plants under AP67. The high difference in the Ci/Ca ratio between normally irrigated and water stressed plants in treatment AP67 indicates poor CO_2 fixation during drought stress. Low CO_2 fixation in treatment AP67 was evident as low photosynthetic rate in the water stressed plants (Figure 10).
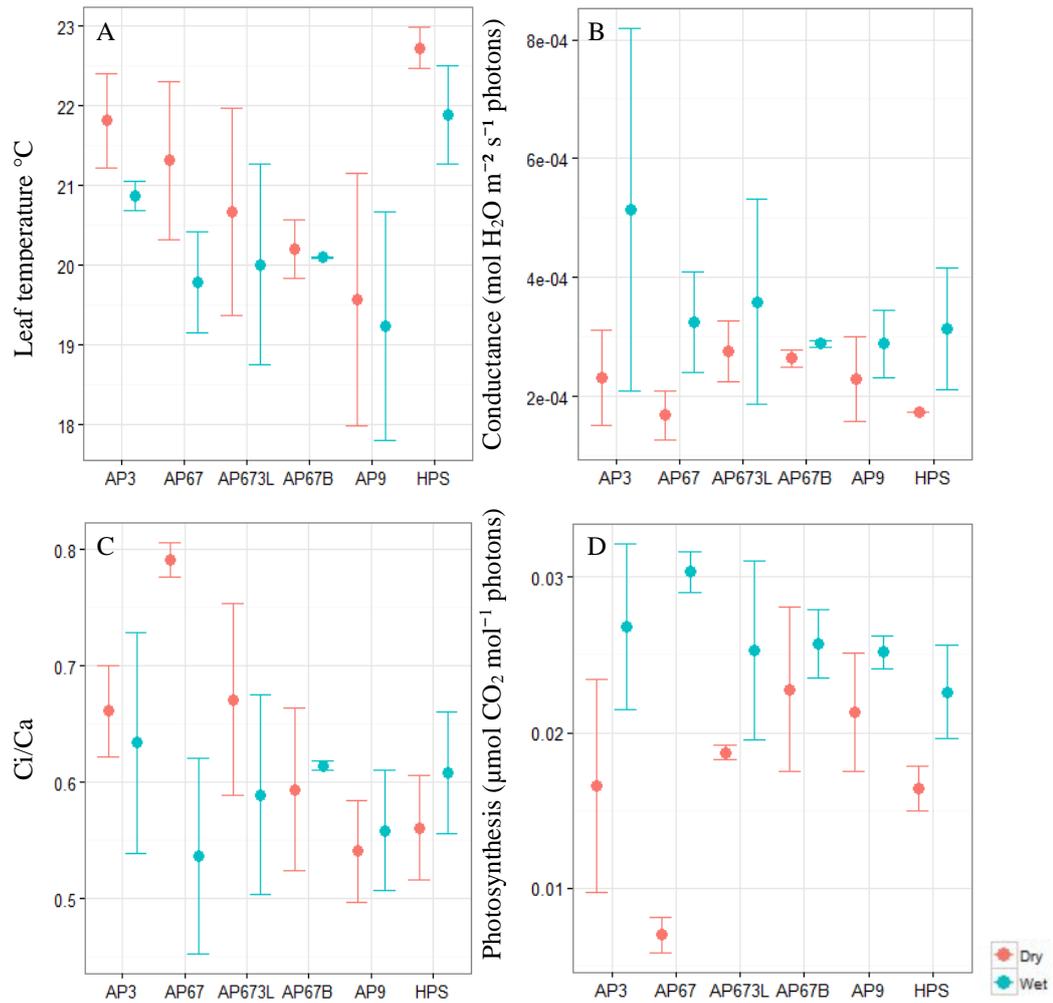
Figure 10 A = Leaf temperature, B = stomatal conductance, C = ratio between CO_2 concentration in stomatal cavity and CO_2 concentration in the atmosphere (Ci/Ca), D = photosynthesis, in light treatments AP3, AP67, AP673L, AP67B, AP9, and HPS. Data are means of 4 measurements ±1SE, except in A, in which the data are means of 16 measurements ±1SE. A = The effect of drought was statistically significant (***P* <0.001**), as well as the interaction effect of light treatment and drought (***P* = 0.041**). B = The effect of drought was statistically significant (**P = 0.0034**), the interaction between light treatment and drought was not statistically significant (P = 0.5086). C = The effect of drought was not statistically significant (P = 0.0828), however the interaction between light treatment and drought was (**P = 0.0493**). D = The effect of drought was statistically significant (***P* < 0.0001**), as was the interaction between light treatment and drought (***P* = 0.0086**).

Leaf temperature was measured during water deficit to test, whether the stomatal conductance differed between light treatments during water deficit. Violet, blue, and red waveband irradiation continued to have a negative correlation with leaf temperature during water deficit (Table 17), however the correlation with violet and blue was not as significant as prior to water deficit treatment. Prior to water deficit, green light and leaf temperature did not correlate, during drought there was a significant positive correlation between them. In addition to green, also yellow light had strong positive correlation with leaf temperature during drought, this correlation was already evident before drought treatment.

Table 17 Correlations between percent contribution of different wavebands to total photon irradiance, R:FR photon irradiance ratio, B:G photon irradiance ratio, Pr:Ptotal ratio, CRY2 effective photon irradiance, and stomatal conductance dependent variables (leaf temperature ºC, photosynthesis, conductance, and CWSI). Stable values of photosynthesis and stomatal conductance were divided by the incident PAR photon irradiance, in order to correct for the differences in the incident PAR. Values are from water stressed plants only. Degrees of freedom in R:FR photon irradiance ratio and leaf temperature are 73, photosynthesis and conductance 18, and CWSI 19. Significance level: * *P<0.05, **P<0.01, ***P<0.001*.

	Leaf temperature Df = 89	Photosynthesis Df = 22	Conductance Df = 22	CWSI Df = 23
Violet	**-0.30****	0.07	0.03	**0.57****
Blue	**-0.26***	0.03	-0.02	**0.53****
Green	**0.23***	-0.15	0.01	-0.15
Yellow	**0.49*****	-0.144	-0.20	**-0.41***
Orange	0.21	0.07	0.13	**-0.45***
Red	**-0.47*****	0.13	0.13	0.37
FR 700-750 nm	-0.046	-0.01	0.03	-0.31
FR 750-800 nm	0.17	-0.10	-0.17	**-0.44***
R:FR	0.15	-0.08	0.03	0.18
B:G	**-0.36*****	0.18	-0.06	**0.58****
Pr:Ptotal	0.08	0.04	-0.00	0.25
CRY2:light	-0.12	-0.02	-0.05	**0.46***

9.4.3 CWSI and ABA

The CWSI was calculated from the data recorded by the thermal imaging camera. The CWSI describes the relative evaporation rate; the lower the CWSI value the lower the evaporation rate is. Highest CWSI value on average in the normally irrigated plants was measured in treatment AP9, in which the CWSI was 0.56. CWSI declined in all light treatments due to water stress, especially in treatment AP67, where the CWSI value was 65 % smaller in water stressed plants than in normally irrigated plants. During water deficit, treatment HPS had the lowest CWSI on average (Table 18).

Table 18 Effect of water deficit on CWSI. Mean values are calculated from 4 plants per treatment ±1SE. Difference (%) is calculated from the mean values between the normally irrigated (Wet) and water stressed (Dry) plants.

Treatment	CWSI		Difference (%)
	Wet	Dry	
AP67	0.50 ±0.22	0.17 ±0.14	-65
AP3	0.36 ±0.07	0.27 ±0.13	-25
AP9	0.56 ±0.07	0.48 ±0.14	-13
AP67B	0.31 ±0.12	0.27 ±0.13	-12
AP673L	0.31 ±0.10	0.24 ±0.16	-22
HPS	0.41 ±0.09	0.16 ±0.15	-61
Statistics			
Treatment	$F_{5,6} = 2.6$	$P = 0.1421$	
Drought	$F_{1,6} = 7.9$	$\textbf{\textit{P} =0.0304}$	
Treatment:Drought	$F_{5,6} = 0.8$	$P = 0.5710$	

The ABA content measured from normally irrigated plants and water stressed plants in each light treatment is presented in Figure 11. In general, the ABA content was higher in the water stress treated plants than in the normally irrigated plants, however, differences were not statistically significant.

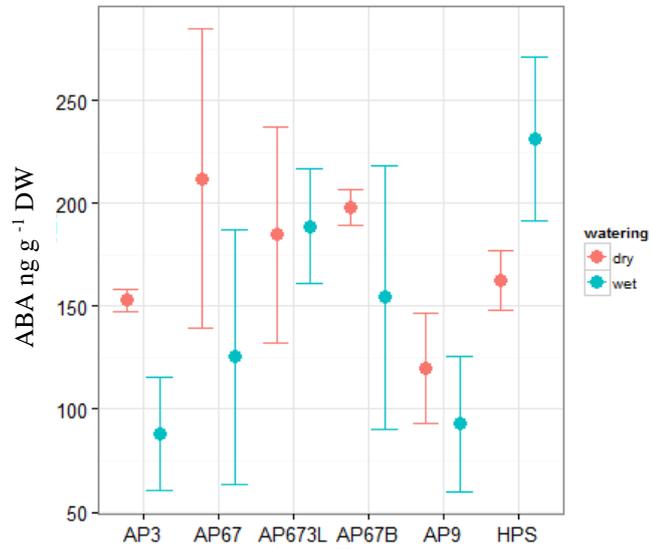Figure 11 Effect of drought treatment on ABA content in light treatments AP3, AP67, AP673L, AP67B, AP9 and HPS. The effect of drought on ABA content was not statistically significant (P = 0.2745), neither was the interaction of light treatment and drought (P = 0.5963). Leaf samples for ABA content analysis were collected during the water deficit treatment. The values in the figure are means of six samples ±SE.

Leaf temperature measured from water stressed plants did not correlate with photosynthesis, conductance, CWSI, or ABA content. Photosynthesis positively correlated with conductance, Ci/Ca and CWSI values. CWSI and ABA had negative correlation; the higher the CWSI value, the lower the ABA concentration in water stressed plants (Table 19).

Table 19 Correlation matrix between leaf temperature, photosynthesis, conductance, Ci/Ca ratio, CWSI, ABA content, chlorophyll content and upper epidermal flavonoids. Stable values of photosynthesis and stomatal conductance were divided by the received PAR amount, in order to eliminate the differences in the received PAR. Values are from water stressed plants only. Significance level: *** *P*<0.05, **P<0.01, ***P<0.001**.

		(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)
Leaf T ºC (1)	r	1	-0.3	-0.2	0.3	0.3	0.2	0.1	-0.2
	df	89	22	22	22	22	10	87	81
Photos. (2)	r		1	**0.76*****	**0.6****	**0.43***	-0.2	-0.1	0.2
	df		22	22	22	22	10	22	20
Conduct. (3)	r			1	-0.0	**0.4***	-0.1	-0.1	0.1
	df			22	22	22	10	22	20
Ci/Ca (4)	r				1	-0.35	0.2	-0.2	**-0.4***
	df				22	22	10	22	20
CWSI (5)	r					1	**-0.6****	-0.4	0.3
	df					23	10	23	21
ABA (6)	r						1	-0.1	-0.4
	df						10	10	10
Chl. (7)	r							1	0.1
	df							91	82
Flav. (8)	r								1
	df								85

9.4.4 Leaf total chlorophyll content

The total leaf chlorophyll content was measured prior to and during water deficit from all plants, from same leaves, in order to examine the effect of water stress on chlorophyll content under different light qualities. The chlorophyll content differences between normally irrigated plants in different light treatments were evident. It was also observed, that the measuring date affected the chlorophyll content of the plants; regardless of drought treatment, the chlorophyll content generally increased over time (Figure 12).
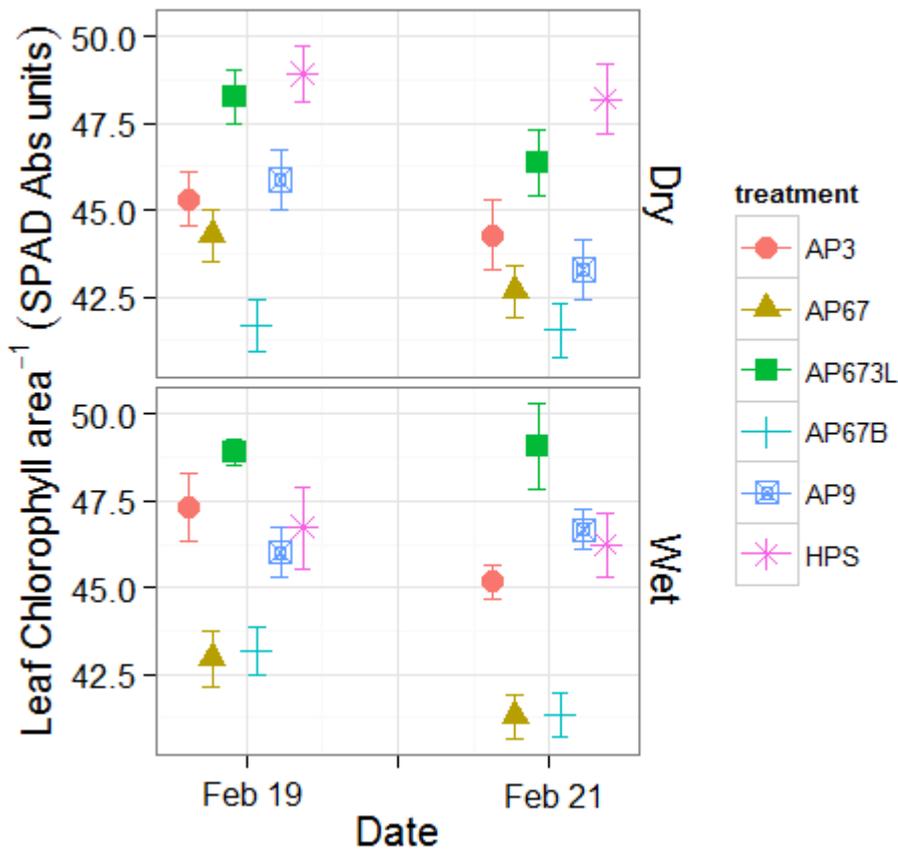

Figure 12 The effect of light treatment, drought, and measurement day on the total leaf chlorophyll content measured in SPAD units. The effect of light treatment on leaf chlorophyll content was significant (**$P = 0.002$**), whereas the effect of drought did not have a statistically significant impact on leaf chlorophyll ($P = 0.321$). However, interaction effect of drought and light treatment had a statistically significant impact on leaf chlorophyll (**$P = 0.022$**). The effect of measurement day was statistically significant (**$P = 0.002$**), but the interaction effect of measurement day and drought treatment was not ($P = 0.518$).

9.4.5 Total flavonoid content in the upper epidermis

Flavonoid content was measured prior to and during water deficit from the same leaves in each water stress treated plant, in order to record the effects of water stress on flavonoid accumulation in the leaf epidermis. Epidermal flavonoid content of the drought treated plants decreased 19 to 26 % in all treatments, except AP9 and AP3, in which the flavonoid content increased 2 and 11 %, respectively. The effect of drought treatment was statistically significant as was the interaction between light treatments and drought. However, when the normally irrigated plants were also taken into consideration, as a "Time –effect", it was shown that the effect of time on flavonoid content was statistically significant as well. Similarly to the water stressed plants, the flavonoid content of the normally irrigated plants decreased in all light treatments between measurement days 2 to 12 %, except in treatment AP9, in which the flavonoid content increased only slightly (Figure 13).
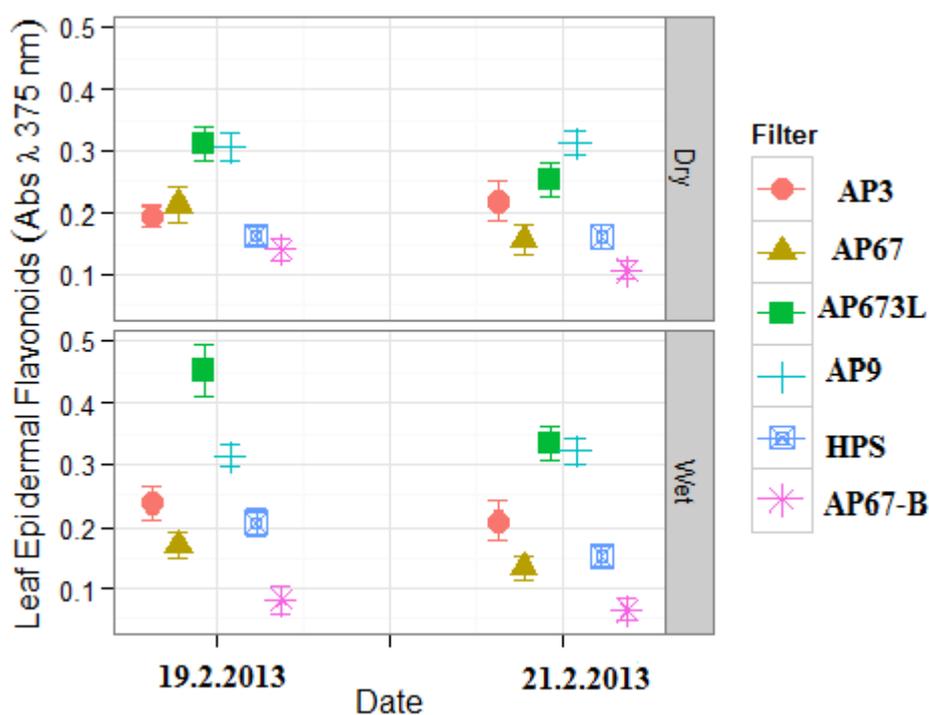

Figure 13 Total flavonoid content of the leaf upper epidermis prior to (19.2.2013) and during (21.2.2013) water deficit measured from normally irrigated plants (Wet) and water stressed plants (Dry). Values are means from 16 measurements ±1 SE. Statistcis: Treatment $F_{5,6} = 23.99$ ***P < 0.001***, Drought $F_{1,12} = 5.13$ ***P = 0.042***, Time $F_{1,6} = 14.75$ ***P = 0.009***, Treatment:Drought $F_{5,12} = 6.55$ ***P = 0.004***, Treatment:Time $F_{5,6} = 2.88$ *P* = 0.115, Drought:Time $F_{1,12} = 1.61$ *P* = 0.229, Treatment:Drought:Time $F_{5,\ 12} = 0.88$ *P* = 0.524.

The SPAD chlorophyll absorbance value positively correlated with orange wavelengths and Pr:Ptotal ratio, whereas red and far-red (700–750 nm) negatively correlated with the SPAD values. Flavonoid content continued to correlate positively with short wavelength irradiance and negatively with far-red irradiance during drought. Also yellow and orange had a negative correlation with flavonoid content, however, the negative correlation between flavonoid content and green waveband irradiation in normally irrigated plants was no longer evident during drought (Table 20).

Table 20 Correlations between percent contribution of different wavebands to total photon irradiance, R:FR photon irradiance ratio, B:G photon irradiance ratio, Pr:Ptotal ratio, CRY2 effective photon irradiance and leaf chlorophyll and total flavonoid contents. Values are calculated from the water stressed plants only during drought. Degrees of freedom in R:FR and SPAD-value is 85 and flavonoids 70.

	SPAD-value Df = 91 or 85	Flavonoid Df = 85 or 70
Violet	-0.1	**0.5***
Blue	-0.0	**0.5***
Green	-0.1	-0.1
Yellow	**0.4***	**-0.2***
Orange	0.3	**-0.2***
Red	**-0.5***	0.0
FR 700–750 nm	**-0.3****	**-0.5***
FR 750–800 nm	-0.1	**-0.6***
R:FR	0.0	**0.3***
B:G	-0.1	**0.5***
Pr:Ptotal	**0.4***	**0.5***
CRY2 eff. photon irradiance	0.1	**0.6***

10 DISCUSSION

10.1 Light quality affects growth and morphology of tomato seedlings

As the photon flux density was set to ~150 µmol·m^{-2}·s^{-1} in all light treatments but plant growth under light of different spectral quality was very different, we can infer that light quality was the main cause of the responses observed.

10.1.1 R:FR and B:G photon ratios regulate plant morphology

Low B:G and R:FR photon ratios have been connected with a shade avoidance syndrome, which involves elongation of stem and leaf petioles (Franklin and Whitelam 2005, Zhang et al. 2011, Sellaro et al. 2010). Our data support this finding, since the longest petioles and stems were in plants grown under the AP67B lamps with the lowest B:G ratio and lowest R:FR photon ratio. In addition, the shortest stem and petiole length was observed in plants grown under AP9 light. AP9 had the highest B:G photon ratio (169.961) which was reflected in inhibition of elongation growth of the stem and petioles. In addition, treatments AP3 and AP9 had the highest Pr:Ptotal ratio, which was evident as short stem length and short internodes.

Green light has been reported to enhance seedling stem elongation and increase the growth rate of young seedlings (Folta 2004). In a study by Folta (2004), seedlings were reported to sense green light, which was apparent as a rapid increase in growth rate after only 15 minutes of green light exposure. Growth was up to 150 % faster in the green light treated plants than in the dark grown seedlings. Folta (2004) suggests that green light complements other, elongation growth inhibiting, blue and red light responses, regulating the growth rate of young seedlings in natural environments. Treatment AP3 had the highest G:PAR photon ratio (0.259) in our experiment. However the highest G:PAR ratio did not result in tallest seedlings, but in fact treatment AP67B, with a G:PAR ratio only 0.128, had the tallest seedlings. This result can be partially explained by the B:G photon ratio differences between these two spectra; the B:G ratios of AP3 and AP67B are 0.751 and 0.011 respectively. In addition to the differences in the B:G photon ratios of these two spectra, the R:FR photon ratio of AP3 was significantly higher than that of the AP67B

(30.300 and 2.575, respectively). Previous studies suggest that the actual portion of green light in the spectrum is not as important as the blue:green ratio for stem elongation growth (Sellaro et al. 2010). The effect of the B:G ratio on stem and leaf elongation can further be supported by results under treatments AP67 and AP67B. Treatment AP67 had B:G ratio of 1.114 and B:PAR ratio of 0.136, and when blue light was omitted from the spectrum, plant height and total leaf area increased 5 % and 12 %, respectively.

Furthermore, Sellaro et al. (2010) claim, that low R:FR ratio has a greater impact on elongation growth than low B:G ratio. This may explain the growth differences between treatments AP3 and AP67. The B:G and R:FR ratios of AP3 and AP67 are 0.751 and 1.114 and 30.300 and 2.733, respectively. The very high R:FR ratio of AP3 caused inhibition of stem and petiole elongation outweighing the effect of low B:G in the spectrum. In treatment AP673L, the R:FR ratio was 6.501 and B:G ratio 1.846, the seedlings of AP673L were taller than AP3 but smaller than AP67. Seedlings grown under HPS lamps were taller on average, than the AP67 seedlings, even though the R:FR ratio of the HPS treatment (3.149) was higher than the AP67. This result can be explained by the lower B:G ratio of HPS (0.230). According to these results, the R:FR ratio did not outweigh effect of B:G ratio, when the B:G ratio is lowered under a certain threshold, however this finding should be explicitly corroborated. Furthermore, the spectrum of HPS contained the most yellow (550–600 nm) wavebands, 42.5 % of the total radiation. Supplemental yellow wavebands have been shown to decrease the total leaf-area and increase both hypocotyl and internode length of tomato seedlings (Braizaityte et al. 2010). The HPS seedlings in our experiment had the second tallest stems and longest internode length. However, it must be remembered, that the R:FR ratios in our experiment were relatively high compared to the R:FR ratios measured outdoors in the natural environments. The typical daylight R:FR ratio measured by Holmes and Smith (1977) is only about 1.15.

Fresh weight strongly correlated with plant height; the taller the plants were, the higher their fresh weight. Blue, violet, and red wavebands caused stem elongation inhibition in seedlings grown under AP9 and AP3 seedlings, resulting in smaller fresh weight than in other treatments. In general, low B:G and R:FR ratios promoted elongation growth of both petioles and leaf blades, which resulted in higher leaf area and therefore higher fresh weight. Plants with elongated shoot, leaf petioles and blades contain more water in

relation to plants which have short stems and smaller leaf area. High water content results in higher fresh weight, however the dry matter content of the smaller, more "compact" plants is normally higher.

The highest number of flower buds was recorded in treatments AP67B and AP67, in which the seedlings had nine flower buds on average, whereas the lowest flower bud number was recorded from treatment AP9, in which on average had just two buds. Treatments AP67B and AP67 had the lowest R:FR photon ratios whereas AP9 did not contain FR at all, therefore having the lowest Pr:Ptotal ratio. This result agrees with those previous studies where prolonged exposure to a low R:FR ratio have induced flowering in many species (Halliday et al. 1994).

10.1.2 Flavonoid synthesis is increased by blue light

Blue light has been reported to increase the flavonoid content of leaves. These compounds have a role in the detoxification of free radicals (Agati and Tattini 2010). In a study by Li and Kubota (2009), FR and G wavelengths were shown to decrease the total upper epidermal flavonoid content in lettuce leaves, whereas UV-B, B, and R were shown to increase the total phenolic content. The lowest upper epidermis flavonoid content measured in our study was in treatments AP67B and HPS, which had the lowest B:PAR ratios. The effect of blue light on flavonoid accumulation was also tested with treatments AP67 and AP67B. Flavonoid content was 80 % higher in the blue-light containing treatment AP67 than in the equivalent treatment AP67B with blue light filtered out. Surprisingly, the highest flavonoid content was not measured from treatment AP9, which had the highest blue light fraction (19.4 %), but from treatment AP673L (total B 4.9 %). In our study, there was a strong positive correlation between short wavelength irradiation (400–500 nm) and the total upper epidermal flavonoid content, whereas wavebands between 500 and 700 nm did not show significant correlations with flavonoids. Large long wavelength fractions of the dose, between 700–750 and 750–800 nm, strongly negatively correlated with flavonoid compound accumulation, supporting the results of Kubota and Li (2009). Nevertheless, the results in our study suggest, that flavonoid synthesis is not dependent on blue and far-red wavelengths only, but other wavelengths and possibly the ratios between wavelengths also have an effect, because the highest

flavonoid content was measured from AP673L and not from AP9. Treatment AP673L had a wide, continuous spectrum ranging from 400 to 750 nm, whereas treatment AP9 was composed of two peaks at red and blue wavelengths.

10.2 Light quality affects stomatal conductance and photosynthesis

Stomatal function was studied by measuring the leaf temperature of the tomato plants grown in different light quality conditions as a proxy. Stomatal closure and photosynthesis are dependent on environmental cues, such as light quality and water availability in the root zone as well as air humidity. The plant hormone, ABA, has also been shown to regulate stomatal closure.

10.2.1 Blue and yellow waveband irradiation regulate stomatal opening

Blue light can induce stomatal opening (Karlsson 1986, Kinoshita et al. 2001, Frechilla et al. 1999); leaves with open stomata allow higher rates of transpiration, with the energy required for evaporation causing a temperature decrease at the leaf surface. The lowest leaf temperature prior to and during water deficit was measured from treatment AP9, which had the highest fraction of blue wavebands in its spectrum. Treatment AP67B had the lowest fraction of blue light in its spectrum; however the highest measured leaf temperature was found in HPS. This result can be explained by the technological differences of these luminaires; the HPS emits heat more than the LED lamps leading to increased temperatures on the leaf surface. The radiant heat from HPS warms up the leaf surface and the increased leaf temperature is detected by the thermometer. Also, the temperature of the rock wool cubes was higher in the HPS treatment than in the LED treatments, which demonstrates the consequences of the directional thermal radiation emission by the HPS lamps.

In addition to the evident blue light effects on the leaf temperature, other wavebands correlated with leaf temperature as well. HPS spectrum contains 42.5 % of yellow wavebands in its spectrum; correlation between leaf temperature and yellow light was strongly positive. However, the correlation may be partially distorted due to the heat emitted from the HPS lamps. On the other hand, when only the results from the LED

treatments were tested, the correlation between yellow wavebands and leaf temperature was still highly positive and statistically significant (cor = 0.44 $P < 0.0001$ df = 86) and the green vs. leaf temperature correlation was still not significant (cor = 0.05 $P = 0.5908$ df = 86). The limits and definitions for green light vary; in our experiment the spectral distribution is presented for every 50 nm, thus the green area is between 500 and 550 nm. Some photobiology papers refer to green light as wavebands between 500 and 570 nm (Sellaro et al. 2010), which in our experiment is partially in the yellow waveband area. From the results of our experiment, it can be reasoned, that this longer waveband green (550–570 nm) is more effective in stomatal closure than the short waveband green (500–550); the long waveband green is grouped together with yellow light in our experiment and thus probably results in a high positive correlation between yellow wavebands and leaf temperature.

10.2.2 Chlorophyll content was increased by blue, yellow, and orange irradiance

The first LEDs manufactured to match the action spectra of chlorophyll and phytochromes contained red wavebands and had the peak at $\approx$ 660 nm in order to maximize photosynthesis and Pr:Ptotal ratio of phytochromes (Bula et al. 1991). Since these early studies to the present day, our knowledge has grown, and it is now known that plants use all PAR wavebands in signalling, photomorphogenesis, and in photosynthesis. Photosynthesis was highest in treatment AP67 and lowest in treatment HPS. The highest measured total chlorophyll values were in treatments AP673L and HPS, however neither of the two treatments had the highest photosynthesis rate. According to our results, blue, yellow, and orange wavebands positively correlated with the total chlorophyll content, whereas red and far-red waveband irradiation had a negative correlation with the total chlorophyll content. These results are similar to those of Fan et al. (2013), where yellow and blue wavebands increased the chlorophyll content of Chinese cabbage and red light caused a decrease in the chlorophyll content. AP673L and HPS contained high fractions of yellow and orange wavebands, in addition AP673L had blue wavebands, which further increased the chlorophyll content. AP67B and AP67 had the lowest measured chlorophyll contents; in the case of AP67 this was likely due to high FR waveband irradiation, and in the case of AP67B the high FR content, together with the blue waveband deficiency resulted in lowest chlorophyll content of the experiment. The photosynthetic rate

generally positively correlates with measured leaf chlorophyll content per leaf area (Fleischer 1934). In our study, treatment AP673L had the highest chlorophyll content but not the highest photosynthetic rate, and in fact, the differences in photosynthesis between light treatments were not statistically significant when photosynthesis was normalized to the received PAR. In our study, photosynthesis negatively correlated with total chlorophyll content, however the correlation was not statistically significant (cor = -0.25 $P = 0.2491$ df = 21).

10.3 Water deficit tolerance in different light treatments

The number of leaves, plant height, and stem diameter decreased in all light treatments due to the water deficit treatment. Similar results have been reported with tomato in earlier studies (Shinohara et al. 1995). The aim of this study was to examine the effect of light quality on drought tolerance.

10.3.1 Light quality affected drought tolerance

Plants grown under a spectrum rich in green and yellow irradiance were the most tolerant to water stress when measured with vegetative growth parameters. Tomato plants grown under AP3 spectrum, containing photon irradiance between 500 and 600 nm ~40 % of its spectrum, produced the smallest reductions due to water deficit for plant height, fresh weight, dry weight and leaf-area. Treatments HPS, AP67B, AP673L, and AP67 had the largest decrease in fresh weight during water deficit; -33, -29, -29, and -24 %, respectively. The lower in fresh weight resulted from decreased leaf area (-31, -26, -22, and -21 %, respectively) and decreased plant height (-12, -14, -9, and -3 %, respectively). The largest decrease in vegetative growth parameters due to water deficit was under HPS. This result can be partially explained by the fact that taller and larger plants had more biomass and larger leaf area than the small plants, and were therefore more affected by drought (Blum 2011). On the other hand, even though the smallest seedlings in the experiment were grown under AP9 lamps, they were not the most tolerant to drought stress. This result suggests that the size of the seedlings was not the only factor determining the drought tolerance of the seedlings.

10.3.2 Blue and green irradiance together with ABA content affected stomatal conductance during drought

In addition to seedling size, the light quality affected the plants performance during drought. Blue light photoreceptors phot1 and phot2 regulate stomatal opening and the intensity of the response is affected by B:G ratio (Ohgishi et al. 2004, Frechilla et al. 2000). Treatment AP9 had the highest B:G and B:PAR photon ratios, which inhibited stomatal closure and therefore sustained a high transpiration rate even during the drought period. This was evident as a small decrease in leaf temperature during drought, as well as very low or no down-regulation of photosynthetic rate or conductance. The Ci/Ca ratio of the AP9 seedlings decreased only a little during water deficit, indicating efficient carbon fixation.

While blue wavelengths increase stomatal opening, green wavelengths act antagonistically to blue and cause stomatal closure (Frechilla et al. 2000). Treatment AP3 had the highest green wavelength fraction of the total irradiance (16.5 %) as well as the highest G:PAR photon ratio (0.3). AP3 plants exhibited the largest leaf temperature increase during water deficit; an increase in leaf temperature indicates stomatal closure and decreased water loss by evaporation. A small decrease in evaporation and therefore in water loss was reflected in a particularly small decrease in plant fresh weight during drought. In contrast, more complete stomatal closure in response to drought was evident as decreased stomatal conductance, and an associated decrease in photosynthetic rate. In addition to the high G:PAR photon ratio of the AP3, a further 21.9 % of the photon irradiance in treatment AP3 was in the yellow (550–600 nm) region. During water deficit green and yellow wavebands were shown to positively correlate with leaf temperature; the higher the green light fraction in a spectrum, the higher the leaf temperature. The yellow waveband was defined in this study from 550 to 600 nm, however, depending which reference is used, this area can also contain long waveband green light, which may contribute more to the stomatal closure than yellow light does itself.

During drought, plants perceive and respond to environmental cues, acclimating and so avoiding excess water loss. When roots sense dryness in soil, the accumulation of a stress hormone, ABA, begins. ABA is transported from roots to leaves and further to stomatal guard cells, where it affects the turgidity of the guard cells and causes stomatal closure

(Shimazaki et al. 2007, Garcia-Mata and Lamattina 2007). Treatment AP3 and AP9 had the lowest ABA content when compared to other light treatments. In general, ABA concentrations increased or remained stable during drought in all light treatments, except in HPS, in which the ABA content was dramatically lower in the water stressed plants than in the normally irrigated plants. The very high ABA content of HPS treatment may be a result of the excess heat directed to leaves (Daie and Campbell 1981).The ABA content of treatments AP3 and AP67 was more than 40 % higher in the drought treated seedlings than in the normally irrigated seedlings. This large increase may be a sign of a severe water deficit in the case of AP67, and a rapid adjustment to drought in the case of AP3.

In addition to phytohormones, other compounds, such as antioxidants are produced during stress periods to overcome unfavorable conditions by detoxifying stress-induced compounds. The accumulation of flavonoids can increase the water-stress tolerance of tomato plants (Sánchez-Rodrígueza et al. 2011). Overall, the flavonoid content of the upper epidermal cells decreased with time between measurement days. Only in treatments AP3 and AP9 did the flavonoid content increase, which could partially explain the good performance of these seedlings during water deficit.

Whereas plants grown under AP3 and AP9 lamps performed well in drought, seedlings grown under AP67 and HPS showed significant fresh weight loss as well as a decrease in photosynthesis. Leaf temperature increased in both these light treatments during drought, evidently due to stomatal closure. This was reflected in a significant decrease in stomatal conductance, Ci/Ca ratio and photosynthesis in treatment AP67. In treatments AP67 and HPS, the CWSI value of the water stressed plants was more than 60 % smaller than that of normally irrigated plants. HPS and AP67 had the lowest CWSI values during water deficit; low CWSI indicates low evaporation and therefore low tolerance of drought stress. Plants under HPS lamps may have been suffering from the high heat load, caused by the heat emitted from the light source. Together with drought, heat may have affected these plants' performance during the drought treatment.

10.4 Seedling quality

At end of this study, the tomato seedlings differed in size and shape. In addition to the morphological differences, the seedlings responded differently to water deficit. For a tomato seedling producer or a tomato grower, a good quality seedling is vigorous, with many leaves, large leaf area, and firm stem. Also the number of flower buds and the time of flowering are valuable information for estimating the yield.

The most compact seedlings were grown under the AP9 spectrum. This result was expected, because the AP9 spectrum consisted of solely blue and red wavebands. Kadman-Zahavi et al. (1976), noted that removal of far-red wavebands from a spectrum causes reduction in elongation growth and hinders flowering. Tomatoes grown under the blue-red spectrum of the AP9 had the shortest internodes and lowest number of flower buds. The exclusion of green wavebands further promotes a compact growth habit; green light is linked to a shade avoidance syndrome (Zhang et al. 2011), in which stem and petiole elongation is promoted. According to our results, the best quality tomato seedlings cannot be cultivated under solely blue and red wavebands which produce seedlings with an overly compact growth habit and delayed flowering. Growth rate under AP9 was slow, thus the growth period to reach a certain seedling size would be prolonged.

The largest seedlings were grown under the LED lamp type AP67 accompanied with a blue-light-removing filter (AP67B) and under the HPS treatment, when measured by plant height and fresh weight. In both cases, the low B:G ratio caused elongation of the stem and leaf petioles, therefore the best quality seedlings were not necessarily the largest ones. The elongation response of the tomato seedlings grown under blue-light-deficit conditions was expected; after all, similar results have been obtained since 1970's (Kadman-Zahavi et al. 1976). In our experiment, the effect of blue light on shoot elongation was directly tested by comparing the AP67 and AP67B to each other, since they share the same spectrum apart from the blue waveband irradiation. Due to blue light removal, plants were taller, fresh and dry weight increased but dry matter content decreased: leaf petioles and leaf blades were longer causing an increase in the leaf area. Elongation of leaves, petioles, and stem are all symptoms of a shade avoidance syndrome, which occurs in environments where R:FR and/or B:G photon ratios are low. It could be possible that seedlings grown under AP67B also suffered because of the water deficit due

to the shade avoidance syndrome; the fresh weight of the water stressed plants was 29 % smaller than the normally irrigated plants, indicating poor drought tolerance.

Dry matter content is given by the ratio of plant dry mass to fresh mass; the higher this ratio the lower the water content of the plant. Healthy, dark, thick leaves generally have higher dry matter content than thin, unhealthy leaves. Therefore, plant condition and growth rate can be partially evaluated by the dry matter content of the shoot. In this study, the highest dry matter content was measured in treatments AP9 (8.8 %) and AP673L (8.8 %), which reflect the good condition of these seedlings. An addition of 10 % of blue wavelengths to a light source has been reported to be the optimum blue light fraction in a spectrum for dry matter accumulation (Goins et al. 1997, Urbonaviciute et al. 2007). Treatments AP9, AP3, and AP673L had B:PAR ratios of 0.531, 0.194, and 0.134, respectively; however the dry matter content in treatment AP3 was lower (7.9 %) than in AP673L. This result indicates, that B:PAR photon ratio alone does not determine dry matter accumulation, but that other wavelengths of the spectrum also affect it. AP3 and AP673L had G:PAR photon ratios of 0.259 and 0.072, respectively, thus the B:G ratios of AP3 and AP673L were 0.751 and 1.846, respectively, indicating that the fraction of green wavelengths in a spectrum inhibits the dry matter accumulation mediated by blue wavelengths. From these results we can speculate, that a B:PAR photon ratio higher than 0.1 does not increase the dry matter accumulation, if the spectra solely consists of red and blue wavelengths.

Plants grown in low R:FR have been reported to flower earlier than plants grown in high R:FR (Halliday et al. 1994). AP9 and AP3 had high R:FR ratios, whereas the other treatments produced lower R:FR ratios. This dichotomy was reflected as decreased number of buds in AP9 and AP3 plants. Treatments AP67 and AP67B had the lowest R:FR ratios, thus highest bud number. The plants growth stage can be evaluated by the time of flowering and by the number of flowers. From the results here, it is apparent, that spectra with high R:FR prolong the vegetative growth stage of tomato, whereas spectra with low R:FR photon ratio induce flowering and a transition from the vegetative to the generative growth stage. For a tomato grower, the timing of flowering is important; prolonged vegetative growth is undesirable, because yield is delayed and possibly reduced.

The transportation of seedlings can be a problem if plants are tall and stems and petioles are not firm. Broken petioles and cuts in stems can allow pathogens to enter; furthermore, a cut stem is no longer useful for cultivation. The seedlings grown under the AP9 lamp had short stems with short internodes; leaves were small and thick with short petioles. This type of seedling would be suitable for transportation. However, their small size may cause a prolonged cultivation time and therefore hinder yield formation.

The highest chlorophyll content prior to the water deficit treatment was measured from treatment AP673L. Güler and Büyük (2007) studied the relationship between the SPAD value, leaf nitrogen content, and yield in tomato and cucumber. They concluded that the SPAD value is highly positively correlated with the leaf nitrogen content and the total yield. Based on this assumption, the largest potential yield in this experiment would have come from the seedlings grown in treatment AP673L.

11 CONCLUSIONS

In this study, R:FR and B:G photon ratios together formed the main components of the spectrum that affected plant morphology. Low R:FR photon ratio enhanced stem and petiole elongation, a response which was partially reversed by simultaneous exposure to short wavelengths, i.e. blue or violet light. R:FR photon ratio also affected the timing of flowering in tomato seedlings. Green light caused stem and leaf elongation, however the B:G photon ratio was more important than the green photon irradiance itself. Exposure to a low dose in the blue waveband and large far-red waveband fraction negatively correlated with the total upper epidermal flavonoid content. On the other hand, it was evident, that other wavebands and possibly waveband ratios, also affected the flavonoid synthesis. Stomatal conductance was partially controlled by blue and yellow waveband irradiation when plants were receiving normal irrigation. Blue, yellow, and orange waveband irradiation positively correlated with total leaf chlorophyll content, and red and far-red waveband irradiation were negatively correlated with chlorophyll content. High chlorophyll content is generally related to high photosynthetic rate, however in this study the chlorophyll content did not correlate with the photosynthetic rate.

In general, smaller sized seedlings have less evaporative leaf area, which results in better drought tolerance. In this study, the smaller seedlings were more drought tolerant than the large seedlings, however the smallest seedlings were not the most drought tolerant, indicating that size was not the only factor determining water stress resistance. The effect of light quality on drought tolerance was examined through stomatal conductance. Blue waveband irradiation was shown to keep stomata open even during drought, which was evident as a small decrease in leaf temperature, photosynthesis and Ci/Ca ratio. On the other hand, yellow and green waveband irradiation caused rapid stomatal closure during drought, which resulted in a lower transpiration rate and thus smaller decrease in biomass. Therefore, seedlings under the spectrum AP3, which contained the most green and yellow waveband irradiation, performed the best under drought conditions. In addition to light conditions, ABA content also affected stomatal closure; in treatment AP3 the ABA content was 40% higher in the drought treated plants than in the normally irrigated plants. Plants under treatments AP67 and HPS had the poorest performance during drought, which was shown as a significant relative mass loss and decrease in photosynthesis. The

drought treatment may have been more stressful to the seedlings grown under HPS, because of the emitted heat from the light source.

AP9 spectrum resulted in extremely compact tomato seedlings, which would be suitable for transportation, but on the other hand would need an undesirably long cultivation period due to their slow growth rate. Seedlings grown under AP673L spectrum did not show an elongated growth habit; growth was well balanced, which was evident as high dry matter content. In addition, the total chlorophyll content was highest in the AP673L spectrum, which indicates adequate nitrogen uptake and translocation, which is important for growth and yield formation.

12 ACKNOWLEDGEMENTS

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APPENDIX 1 A MAP OF THE EXPERIMENTAL LAYOUT

| Table 1 | Table 2 | Table 3 | Table 4 |

AP67				AP67Blue				AP9				HPS			
D	W	D	W	D	W	D	W	D	W	D	W	D	W	D	W
W	D	W	D	W	D	W	D	W	D	W	D	W	D	W	D
D	W	D	W	D	W	D	W	D	W	D	W	D	W	D	W
W	D	W	D	W	D	W	D	W	D	W	D	W	D	W	D

AP3				AP67				HPS				AP673L			
D	W	D	W	D	W	D	W	D	W	D	W	D	W	D	W
W	D	W	D	W	D	W	D	W	D	W	D	W	D	W	D
D	W	D	W	D	W	D	W	D	W	D	W	D	W	D	W
W	D	W	D	W	D	W	D	W	D	W	D	W	D	W	D

AP9				AP673L				AP67Blue				AP3			
D	W	D	W	D	W	D	W	D	W	D	W	D	W	D	W
W	D	W	D	W	D	W	D	W	D	W	D	W	D	W	D
D	W	D	W	D	W	D	W	D	W	D	W	D	W	D	W
W	D	W	D	W	D	W	D	W	D	W	D	W	D	W	D