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Effects of light spectra on plant growth and development

Bachelor's Thesis

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Declaration

I hereby declare that I have authored this bachelor's thesis carrying the name "Effects of light spectra on plant growth and development" independently under the guidance of my supervisor. Furthermore, I confirm that I have used only professional literature and other information sources that have been indicated in the thesis and listed in the bibliography at the end of the thesis. As the author of the bachelor's thesis, I futher state that I have not infringed the copyrights of third parties in connection with its creation.

In Prague on May 5, 2021 ______________________________

Acknowledgments

I would like to thank my supervisor doc. Ing. Pavel Klouček for his time and guidance.

Effects of light spectra on plant growth and development

Summary:

This paper is a review on the effects of spectral quality (wavelengths of light) on plant growth and development. We report effects of photosynthetically active radiation (PAR 400-700 nm) divided into blue light, green light and red light. In a first part, plant responses to changing light spectra are examined for each light colour in the PAR region, including the varying effects of broad spectrum lights (combination of wavelengths) and monochromatic lights (single wavelength) on different species. The second part focuses on plant responses to radiation outside the PAR region. In this part we report effects of far-red light and ultraviolet light. While spectral quality describes the colours of light, plant responses are also altered with spectral intensity. We use photosynthetic photon flux density (PPFD) as a light intensity measurement unit for this paper and explore the effects of spectral quality at different PPFD. In a third part, we take a closer look to one species, *Cannabis sativa*. A plant which is most commonly grown in closed systems under artificial light.

Keywords and Acronyms:

BL, Blue Light

GL, Green Light

RL, Red Light

FR, Far-Red

UV, UltraViolet

PAR, Photosynthetically Active Radiation

PPFD, Photosynthetic Photon Flux Density

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1 Introduction

Until very recently, studies showed that agriculture started some 12,000 years ago in the Levant, a region where some of the earliest known human civilisations were established. However in 2015, the collaborative research led by Tel Aviv University and Harvard University found evidence that trial plant cultivation began far earlier, some 23,000 years ago (Snir, 2015). The main components that made this nook of the world into the cradle of agriculture are its special conditions of Sun and soil. The Sun is the main source of light and heat for our planet. Plants use photons of sunlight to trigger photosynthesis and produce energy for their life cycle. Humans have evolved to learn how to recreate and control many natural phenomena artificially, including artificial lighting to grow plants. Centuries of advancements in technology, like the making of specialised machines and instruments made it possible to study light and manipulate its spectrum for better understanding plants' light requirements.

Research in photobiology began in early 19th century with primitive light sources and coloured filters (Wassink, 1956). These pioneer experiments identified photoreceptors and action spectra for specific region of light that regulate plant growth and development. In this paper we will try to understand how plants respond to different wavelengths of light and how their growth and development are affected. We will distinguish the terms growth and development as plant growth, that is an increase in dry weight of the plant, which directly comes from photosynthesis and plant development, that is the shape of the plant, the morphogenesis. Studies show that spectral quality has an effect on photosynthesis but the effect it has on plant photomorphogenesis is much bigger. When manipulating ratios of light colour, the primary effects are expected to alter the shape of the plant rather than the rate of photosynthesis. Plant shape varies among species, different species have different responses to spectral quality but photosynthesis among species varies much less (Cope, 2014).

Radiation is the source of energy for photosynthesis, and provides information for photomorphogenesis (Smith, 2013). Photosynthetically Active Radiation (PAR), 400 nm to 700 nm, is the numerical representation of the portion of light spectrum that drives photosynthesis. Plants capture photosynthetically active radiation by using pigments that have specific action spectra. The most active pigment in photosynthesis is chlorophyll A that is responsible for capturing violet-blue (peak absorption at 430nm) and red (peak absorption at 660nm) colours. Chlorophyll B is an accessory pigment and is responsible for collecting light energy and passing into chlorophyll A, the most efficiently absorbed wavelength by chlorophyll B is 470 nm, which is blue light. Other accessory pigments include carotenoids that contribute to photosynthesis by transferring absorbed energy (Freeman, 2002). Photosynthetic photon flux density (PPF or PPFD, sometimes used interchangeably) is a measurement of the total amount of light in the PAR zone that is produced by a light source on a square meter each second and is given in $\mu mol.m^{-2}.s^{-1}$. Studies in the 1970’s gave equal weight to all photons in the PAR zone, but not all photons are equally efficient in driving photosynthesis (McCree, 1972b)

The McCree curve is one of the most cited papers in current photobiology and light quality research. The curve is the results of experiments led by Dr Keith McCree in the 1970's on relative quantum efficiency and shows a function that quantifies the average photosynthesis response of plants to light between 350nm and 750nm. This experiment defined the range of PAR and indicated that red light (600-700 nm) is 25 to 35 % more efficient than blue light (400-500 nm) and 5 to 30 % more efficient than GL (500-600 nm) in driving photosynthesis. However scientists, including McCree knew that wavelengths outside the PAR zone could also be beneficial for photosynthesis (McCree, 1972a). McCree’s measurement were on single leaves and at low PPF and with added wavelengths of light on monochromatic backgrounds. Therefore general conclusions on whole plant responses at different PPF and with mixed colours of light cannot be represented with these results. The curve also shows photosynthesis efficiency but not the combined effects of photosynthesis and development.

Photomorphogenesis can be defined as the development of the shape of plants in response to changes in light spectrum and is regulated by types of photoreceptors such as phytochromes, cryptochromes, and phototropin (Briggs, 2001). Phytochromes are responsive to red and far-red radiation, cryptochromes to blue and ultraviolet-A, and phototropins to blue, green and ultraviolet-A. The interaction of photoreceptors, depending on the radiation received by the plant, may broaden the range of light spectrum that the plant can use but may also have antagonistic effects. Their activity can be manipulated by changing light spectra (Casal, 2003).

In recent years, with the introduction of light emitting diodes (LEDs) the research on photobiology evolved to control and reorganise spectral quality in ways that have been difficult with conventional electric light sources. The versatility, the high energy efficiency, the long life and the possibilities to test the effects of different spectral combinations of wavelengths on plant growth and development are among the advantages of new LED technologies (Backer, 2019). This implication could lead to determining an optimal light emission spectrum for plant life while minimising energy costs (Tamulaitis, 2005). In the last 20 years, studies have exploited the spectral elasticity of LEDs and observed plant responses to changing wavelengths of light.

2 Aim of Study

Despite decades of research, the effects of spectral quality on plant growth and development are not well understood. The aim of this paper is to gather results of research on effects of light colours on plants and further elucidate the ongoing research on plants‘ light requirements.

3 Litterature review

3.1 Effects of Photosynthetically Active Radiation (PAR, 400-700 nm)

3.1.1 Effects of Blue Light (BL, 400-500 nm)

Although red light is efficiently used for photosynthesis, some blue light is typically necessary to improve growth and minimise shade avoidance responses, like excessive stem and internode elongation (Dougher, 2001/Kim, 2005). The amount of BL required to promote normal growth and development varies among species and can be expressed as the absolute amount of BL, which is amount of photons between 400 and 500 nm and is given in µmol.m^{-2}.s^{-1}, or as the relative amount of BL which is given as a percent of the total PPF (Cope and Bugbee, 2013). Wheeler (1991) was the first study to propose that plant developmental response to blue light was dependent on absolute BL rather than the relative amount of BL for stem length in soybean. The research concluded that approximately 30 µmol.m^{-2}.s^{-1} of BL is necessary to control stem elongation. Yorio (2001) found that dry mass of radish, spinach and lettuce increased with the addition of 10% BL, the results were similar to Wheeler's and showed that a minimum of 30 µmol.m^{-2}.s^{-1} of BL is required for healthy growth and development. Goins (1997), using the same lighting found that dry mass of wheat with 10% BL was comparable to a white light control (33% BL). On the other hand Hoenecke (1992) indicated that 50 µmol.m^{-2}.s^{-1} or 15% BL (whichever is greater depending on PPF) is the amount of BL that most species need. They also concluded that relative BL is a better predictor of most responses of soybean, wheat and radish. Various results from various studies indicate that further research is necessary to understand absolute and relative BL and determine which can better predict plant growth and development. Varied results also suggest that BL responses are species dependent and that effects of BL ratios and colour interaction in light fixtures still remain unclear.

Too much BL will inhibit cell expansion, crop yields seemed to reach a plateau or even decline as BL fraction reaches a threshold (Piovene, 2015). Numerous studies have explored the limits of BL fractions and found that between 5 and 15% BL, lettuce, radish and pepper yielded the highest dry mass. In addition K. R. Cope and B. Bugbee (2014) indicated that dry mass and leaf area decreased above 15% BL for the same three crops. Naznin (2016) found that fresh and dry mass of coriander, increased when BL increased from 5% to 9% at 120 µmol.m^{-2}.s^{-1} and 16-h photoperiod for 28 days, but decreased when BL was 17%, and the lowest DM was reported under monochromatic red light. Study by Hernández and Kubota (2015) reported decreased dry mass and leaf area for cucumber when the BL fraction increased above 10% with a pure RL background, they also reported that in cucumber dry mass and leaf area decrease continued with increasing BL regardless of the background light colour. In contrast, the fresh weight of sweet basil increased when BL increased from 15% to 59% at 200 µmol.m^{-2}.s^{-1}and 16-h photoperiod for 31 days, and the fresh weight was highest under monochromatic blue light compared with red, green, blue+green, or white light at 100 µmol.m^{-2}.s^{-1} PPF and 16-h photoperiod for 70 days (Amaki, 2011). Dougher and Bugbee (2004) studied the physiological responses of soybean and lettuce to blue photons and came to the conclusion that increased BL inhibited cell expansion and division in the stems and leaves. Many of these studies validate early results from Hoenecke (1992) that showed beneficial effects of supplementing monochromatic red LEDs with blue fluorescent light. but not every experiment gave the same results. A study by Son and Oh (2013), using a pure RL source (0% BL) harvested highest fresh and dry mass of lettuce, but also noted that leaves were chlorotic.

The combination of red and blue lights seems to promote better growth and development compared to monochromatic blue or red light. Mitchell (2015) reported that under pure RL plants developed excessively elongated hypocotyls and cotyledons which is a condition that is phytochrome dependent. Combining red and blue lights resulted in more excited photoreceptors including phytochromes, crytochromes and phototropins which promote growth and development (Sabzalian, 2014).

3.1.2 Effects of Green Light (GL, 500-600 nm)

During the 20th century the emergence of efficient fluorescent lamps made way for various experiments on the interaction of plant and its environment to be carried out. Frits Went, a dutch botanist, gathers his experiments in the book “The experimental control of plant growth” (Went, 1957). Went studied the effect of green light in the growth of tomatoes for a period of only few days and came to the conclusion that full spectrum white light, with a high green photon fraction is less effective than one with mostly red or blue photons. The results of similar experiments during the first half of the century also led to the unfounded consensus that green light is ineffective in photosynthesis. This consensus ruled plant biology and physiology for more than 50 years. Chlorophyll reflects most of the green light but still absorbs a small proportion that play a determinant role. Many of the older editions of plant physiology textbooks persistently mention the inefficiency in photosynthesis of green light when compared to blue and red lights. Today's modern textbooks contain more information about green light absorbing pigments, including phycoerythrobilin (Taiz, 2015) among other photosynthetic pigments and show how green light contributes to the photosynthesis efficiency, especially in certain species, like the macroalgae (Sepúlveda, 2011).

Various studies from the second half of the century onward have shown significant increase in dry matter yield of some species when exposed to green light (Kim, 2004). Lettuce shows great response to the changing light spectrum. An experiment is carried out where one full spectrum LED, one compact fluorescent lamp and one light source with no green photons are used to grow lettuce. At the same PPF, the experiment resulted in higher dry matter in full spectrum lights with green photons (Lin, 2013). Green light penetrates deep into leaves, more so than red and blue lights (Brodersen and Vogelmann, 2010). A study led by Sun (1998) shows how beneficial green light can be in the carbon fixation. Red and blue lights induce CO2 fixation largely in the upper palisade mesophyll and green light in the lower palisade. When the upper parts of the canopy are saturated by red and blue light, green photons continue to be photosynthetically beneficial (Nishio, 2000). A study by Terashima (2009) states that in high PPF, green photons are more beneficial for single leaf photosynthesis than red and blue photons and that supplemental GL can improve plant growth and development.

Kim (2004) reported that GL was detrimental in high (51%) and in low (0%) proportions and that approximately 24% was the proportion required by the species that were studied. Another study by Johkan (2012) experiments with three PPF values using green LEDs and cool white fluorescents. The results in growth response to green light were unstable, as PPF increased stunted growth and developmental abnormalities were observed and above 300 $\mu mol.m^{-2}.s^{-1}$ decrease was reported in dry matter.

Many of the experiments show different effects among species and give different results, this makes it difficult to make general conclusions regarding the effects of green light on plant growth and development. However, obtained results remain very important as, in the search of an optimal light ratio, many of the latest LEDs include a greater fraction of green light compared to older purple fixtures with mostly blue and red and no green photons.

3.1.3 Effect of Red Light (RL, 600-700 nm)

Red light (RL) seems to be more effective in driving photosynthesis compared to blue and green lights (McCree, 1972a). Red photons are well absorbed by leaves, are photosynthetically efficient, and are efficiently generated by LEDs, therefore they are widely used in horticultural light fixtures. Red and blue lights have an essential role in plant growth and development as chlorophyll a and b effectively absorb both red (600-700 nm) and blue (400-500 nm) wavelengths of light (Kusuma, 2020). The absorption of blue and red photons by plants has been measured as 90%, which indicates that plant development and physiology is strongly influenced by blue or red light (Terashima 2009). Red LEDs were effectively increasing plant biomass such as fresh and dry weights, height, and leaf area, while blue LEDs were reported to simulate photosynthetic function and induce the formation and development of chlorophylls, rather than having a direct effect on plant growth (Son, 2013).

Kong (2006) found that supplementary RL for greenhouse grown grape, *Vitis vinifera* cv. 'Jingxiu' increased the leaf area as well as the dry mass distribution ratio in leaves compared to sunlight. Goto (2013) studied the photosynthetic responses of green and red perilla, *Perilla frutescens* a species in Lamiaceae family and a popular herb in East Asia. The study, conducted under different combinations of LEDs (405, 465, 530, 595, 660, and 735 nm), at 250 µmol m-2 s-1 and 16 hour photoperiod for 14 and 21 days resulted in the highest increment of photosynthetic rate, Pg with RL at 660 nm and lowest Pg at 465 and 530 nm. Goto (2013) also reported that both plants grown under red enriched light treatments (pure red, red-blue, red-green) had a greater dry weight that plants grown under blue enriched light treatments. The high efficiency of RL on plant growth is often attributed to the correlation of RL wavelengths and the absorption peak of chlorophylls and phytochromes, therefore supplementing light conditions with RL would be most efficient (Dou, 2017).

Although red photons have a great potential to drive photosynthesis, plants are adapted to utilise a wide spectrum of light to regulate photosynthesis (Kang, 2013). Muneer (2014) studied the responses of lettuce under three monochromatic LEDs, blue, green and red and at two different PPFD, 80 and 250 µmol m−2 s−1. The plants grown at 250 µmol.m^{-2}.s^{-1} showed a significantly higher rate of photosynthesis than plants grown at 80 µmol.m^{-2}.s^{-1} under blue

LEDs. However, the plants grown under red LEDs showed lower rates of photosynthesis with a decrease in light intensity. The lowest rate of photosynthesis was observed for the plants grown under green LEDs with a decrease in light intensity. Yorio (2001) reported that there was higher weight accumulation in lettuce grown under RL supplemented with blue light than in lettuce grown under RL alone. Monochromatic red light has been reported to reduce the photosynthetic efficiency and to lead to photo-damage after long exposures (Trouwborst, 2016). Schuerger (1997) reported that leaf thickness increased when RL was supplemented with blue light. Furthermore, supplementing red light with blue light promotes dry matter production in several plant species, including pepper, wheat, spinach, radish and lettuce (Goins, 1997/Yorio, 2001).

3.2 Effects of radiation outside PAR region

3.2.1 Effects of Far-Red (FR, 700-800 nm)

Research on far-red (FR) effects on plant growth and development is much more recent than studies on traditional photosynthetically active radiation. This emerging field is becoming the focus of many researchers and more companies are adding far-red LEDs into light fixtures. FR light is the range of light at the extreme red end of the visible spectrum, the region between red and infra-red lights, between 700 and 750 (or 780) nm. We cannot see FR photons, they are barely visible to the human eye, and yet they have powerful effects on plants that recent research is discovering. For many years these effects were missed because electric lights do not have FR fractions, sunlight on the other hand is loaded with FR photons but it was not until the introduction of LEDs, and especially FR LEDs that valuable research could be conducted and more and more light fixtures included FR ratios (Runkle, 2001). This work is both fascinating from the standpoint of fundamental plant photobiology, and also as it has immediate significant commercial implications because both photosynthesis and plant shape can be manipulated with FR photons (Park, 2003).

Plants' adaptive responses, such as changes in shape, biochemical composition and developmental stages are directed by spectral quality, quantity and duration of light (Kendrick, 1994). Phytochromes are the red and far-red sensitive photoreceptors and play a centre role in sensing plant shade avoidance responses, which often maximise plant growth and health under dense canopies (Schmitt, 1995). Even before plants receive diffused light and are directly shaded, phytochromes can capture small amounts of additional FR light that bigger plants reflect in the environment. This phenomenon triggers faster stem elongation in shade avoiding seedlings as competition is necessary to reach the light (Casal, 2013). Jorge Casal (2013) also stated that forest understories and dense canopies have a lower Red:Far-Red ratio when compared to direct light. In addition, Franklin (2008) reported that increased stem and petiole growth is a most prominent shade avoidance response. Casal (2012) also studied shade avoiding species adapting to open habitats, he reported that reduced branching and tillering, lower leaf to stem dry mass ratio, smaller proportion of biomass allocation to the roots, hyponastic leaves with reduced chlorophyll content and earlier flowering are among the most frequently observed responses to low R:FR ratios. Some o these shade-avoidance responses can also be induced in agronomic crops under high density monocultures, they are often undesired as they can cause crops to be more prone to drought and lodging and negatively affect yield (Morgan, 2002).

Some species tolerate shade, unlike shade avoiding species they do not undergo any phytochrome-mediated stem extension growth, instead they maximise their light capture through leaf expansion, this can be desirable for leafy agricultural crops. Recent advances in LED technology enable precise control of spectral quality in controlled environment crop production (Massa, 2008). The simulation of shade through FR supplementation may be one of the most powerful effects as the increase of FR can be achieved without reduction of light intensity in the PAR region. One important difference between simulated shade and natural vegetation shade is that natural shade significantly reduces total photon flux (Casal, 2012). FR induced leaf expansion is observed in white clover under high PPFD (320 $\mu mol.m^{-2}.s^{-1}$) but not under low PPFD (110 $\mu mol.m^{-2}.s^{-1}$). A low R:FR ratio induces leaf expansion in most shade simulating studies under medium to high light intensity. In order to promote desired leaf expansion with high fraction of FR photons, an adequate photon flux in the PAR zone is necessary (Valladares, 2008). These recent findings justify the reconsideration of the photosynthetic value of far-red photons.

3.2.2 Effects of Ultra-Violet (UV, below 400 nm)

Ultraviolet radiation sits on the edge of the visible spectrum and with decreasing wavelengths becomes less visible to the human eye and more damaging for plants (Zuk-Golaszewska, 2003). Based on their wavelength, UV lights are divided as UV-A (320-400 nm), UV-B (280-320 nm) and UV-C (below 280 nm). UV radiation is considered a stress factor to plants and generally leads to smaller plants, reduced photosynthetic activity and lower dry weight, but appropriate UV light treatments have been shown to be beneficial for some species. The solar UV spectrum is mostly composed of UV-A radiation while UV-B constitutes only a small fraction. Earth's atmosphere blocks wavelengths under 280 nm hence UV-C radiation from the sun does not reach the surface (Weih, 1998). For closed systems, research has focused primarily on the effects of UV-B lights, as they were shown to have significantly greater effect on plants than UV-A radiation (Barnes, 1988). The limited solar UV-B radiation is a crucial light to which plants can develop photomorphogenic responses, described as change in morphology, physiology and in the synthesis of secondary metabolites (Jenkins, 2009). UV Resistant Locus (UVR8) is the photoreceptor responsible for UV-B induced responses. Short wavelength irradiation was shown to affect plant defence mechanism by inducing metabolic activity, such as the synthesis of phenolic compounds that act as UV screening molecules (Rizzini, 2011). Under UV light, phenolic compounds, including anthocyanins that are found in many red leaf plants, have been observed in high concentration in lettuce (Krizek, 1998). Plants produce phenolic compound as part of their protection mechanism when they are under environmental stress. Short-wavelength irradiation and high photon flux irradiance are examples of light mediated stress and are studied on numerous species. Flavonoids and phenylpropanoids are examples of phenols synthesised by plants that are concentrated in the leaf epidermis and in both the palisade and spongy mesophyll tissues and can reduce the oxidative damage and the penetration of UV radiation to the leaf (Agati, 2013).

Cannabis sativa produces through secondary metabolism, alkaloids known as cannabinoids, that have been reported to be part of the plant's defence mechanism and to have antioxidant properties, they include Δ-9-tetrahydrocannabinol (THC) and cannabidiol (CBD) as well as cannabigerol (CBG) (Hampson, 2000). Different species have different responses to the level of UV-B irradiation (Matthew, 1996). Furness (1999) studied the biennial dicotyledonous plant *Tragopogon pratensis* and reported that vertical leaf orientation and a concealed apical bud can have protective effects from UV-B light. The study showed on the other hand, that *Cynoglossum officinale* resulted in high susceptibility when apicals were exposed to UV-B. Cline and Salisbury (1966) had proposed that the vertical leaf orientation, the protective basal sheath and the concealed apical meristem of monocots protect the plant from UV-C radiation better than dicots. Responses of sweet basil (*Ocimum basilicum*) were studied by Sakalauskaite (2012) who reported that supplemental UV-B on a white background light for both 1 hour and 2 hours per day for seven days increased, plant height, FW, DM and leaf area. It was also reported that the 2 hour UV-B exposure per day had greater effects than the 1 hour treatment. However, Afreen (2005) showed that a long exposure time at a low light intensity or a short exposure at a high light intensity when supplementing with UV-B had negative effects on the photosynthetic rate of Chinese liquorice (*Glycyrrhiza uralensis*) and also reduced DM and leaf area of sweet basil and perilla. Interestingly, under high PPFD lettuce (*Lactuca sativa*) showed increase in net photosynthesis when supplemented with UV-B (Wargent, 2015), likewise UV-B stimulated the photosynthesis rate of Swedish ivy (*Plectranthus coleoides*) and increased CO2 assimilation, stomatal conductance and internal CO2 concentration under both high and low PPFD (Vidovic, 2015).

The plant responses induced by UV-B may influence competition for light and negative effects of UV-B radiation may result in deformed morphology (Barnes, 1988). Furness (1999) reported that exposure to UV-B decreased cell expansion thus plants were smaller and resulted in lower FW, DW and increased tillering and leaf curling. A study by Dai (1995) shows significant reduction in leaf area and plant DW of rice (*Oryza sativa*) after two weeks of UV-B treatment. The effects of light intensity and exposure time of UV radiation on plant growth and development thus seem species dependent and further research is necessary in order to thoroughly understand plant responses to UV lights.

3.3 A closer look to *Cannabis sativa*

Until recently, the production of *Cannabis sativa* was restricted to varieties known for their high fibre quality, but rapidly changing jurisdictions around the world have opened a new window to study medical *Cannabis*. Among horticultural plants, *Cannabis sativa* stands out in that, its total economical yield cannot be rated only by the weight of the flowers but the chemical composition of the end product is also in the interest of the producers and consumers (Magagnini, 2018). The cultivation of *Cannabis* is particularly interesting for the topic of this paper because it is a crop that is mostly grown in closed and controlled sytems, such as growth chambers both for research and commercial practices. Different *Cannabis* varieties contain numerous chemical compounds, such as cannabinoids, that are known to have various pharmacological effects. *Cannabis sativa* flowers are the main source of the cannabinoid Δ-9- tetrahydrocannabinol (THC) used in medicine (Chandra, 2017).

Cannabinoids are a unique class of secondary metabolites synthesised primarily in capitate-stalked trichomes that are concentrated on the bracts of the *Cannabis* flowers, and were first studied by Gaoni and Mechoulam (1965) more than 50 years ago. Today, over 100 cannabinoids have been described and studied (Andre, 2016). The cannabinoid concentration is greatly affected by environmental factors, this has significant importance as the distinction between marijuana (over 0.3% THC) and industrial hemp (below 0.3%THC) is a legal concern and the demand for medical *Cannabis* with traceable and consistent cannabinoid profiles is increasing (Potter, 2014). The beneficial effects of spectral quality on secondary metabolism has been studied on numerous species (Ouzounis, 2015), while light quality may have an effect on the cannabinoid synthesis, *Cannabis* yields are thought to strongly correlate with increasing light intensity (Chandra, 2008). Early work of Fairbairn and Liebmann (1974) on *Cannabis* suggested that PPFD, spectral quality and photoperiod can alter cannabinoid biosynthesis. Mahlberg and Hemphill (1983) used plexiglas filters to obtain monochromatic light for greenhouse grown hemp and found that under red filters plants produced three times higher cannabinoid concentration than plants grown under blue and green filters. They also reported a shift in the ratio of cannabinoids, in particular cannabichromene (CBC) and THC, under monochromatic filters compared to natural sunlight. In the study by Vanhove (2011), it was concluded that *Cannabis* variety and not the cultivation method determined cannabinoid concentration and an increasing irradiance level correlated positively with the dry weight of the plant.

Most spectral studies have investigated plant responses to light spectra at a PPFD of 500 µmol.m^{-2}.s^{-1} or less, but responses to photons can interact with intensity (Cope and Bugbee, 2013), so it is difficult to extrapolate the findings on plant response at low PPFD to intensities greater than 500 µmol.m^{-2}.s^{-1}. This is particularly important with *Cannabis*, which has an increasing rate of photosynthesis above a PPFD of 1500 µmol.m^{-2}.s^{-1} and is increasingly being grown under high PPFD in commercial cultivation (Chandra 2008). In order to achieve an optimal *Cannabis* flower and cannabinoid yield, research on optimal light spectrum needs further development. The effects of abiotic factors on plant growth have been long studied. Chandra (2008) observed the responses of *Cannabis* to changing irradiance, CO2 and temperature levels and reported that photosynthetic efficiency was maximal at 1500 µmol.m^{-2}.s^{-1}, at 750 µmol CO2 mol^{-1} and at 30 C. The study concluded that high light intensity, a high CO2 concentration and dry conditions can promote both photosynthetic activity and water use efficiency. Light quality, intensity, source and photoperiod play a critical role in yield and quality of *Cannabis*. Literature values for *Cannabis* yields, given in grams per Watt of energy consumed, range from 0.3122 to 1.972 g W^{-1} and are influenced by genetics and growing conditions (Potter and Duncombe, 2012). Results from the study by Backer (2019) indicate that increasing the duration of the flowering period (or reducing the duration of the vegetative period) increases yield per square meter and cannabinoid content per square meter. The same results were reported by Vanhove (2012), who also stated that increased photosynthetic assimilation was directed to bud growth instead of stem and leaf growth. Spectral quality can trigger synthesis of secondary metabolites but no theoretical mechanism that links spectral quality to cannabinoid biosynthesis has been reported; the increase in cannabinoid yield was mainly caused by light intensity (Chandra, 2008).

The study by Magagnini (2018) examined the effects of three different light source on the morphology and the cannabinoid production. Cannabis clones were grown under three light treatments, one high-pressure sodium (HPS) and two LED fixtures, AP673L and NS1, at PPFD 450 µmol.m^{-2}.s^{-1} and 18 hour photoperiod during vegetative phase for 21 days and 12 hour photoperiod during reproductive phase for 46 days. Plants under LED lights were shorter and more compact than the ones grown under HPS lighting, which were significantly taller and had higher stem dry weight. No notable differences were observed between the two LED treatments. Plant height and dry stem weight was reported to range from 79,2 cm and 14,2 g in HPS to 54,5 cm and 7,6 g in LEDs respectively. These results are consistent with earlier findings of Wheeler (1991), who stated that plants grown under sole HPS light are more prone to unbalanced and excessive leaf and stem elongation.

4 Conclusion

Plant growth can be defined as the increase of dry matter produced by the plant which is the result of photosynthesis, while plant development can be defined as the change in the shape of the plant, such as stem elongation, leaf and petiole expansion which determine light interception. Plants adapt to the light conditions in their environment and maximise light capture and photosynthetic activity. In this paper we have gathered several of the key findings on plant physiology and photobiology research of the last 60 years. The main conclusions we can draw are as follows;

For most species a multiple wavelength light treatment increase dry mass significantly more than monochromatic blue, green or red.

Blue light inhibits cell expansion. The inhibition of stem elongation is beneficial for many species but leaf expansion inhibition often results in decreased dry mass.

Green light is efficient in denser canopies and facilitates human vision. The misperception that green photons are not efficiently used is disproven and today’s light fixtures have GL fractions.

Red light is very efficient for photosynthesis. Red photons are about 15% more efficient than blue photons in driving photosynthesis.

Far-red light enhances cell expansion. FR photons increase dry mass especially in leafy greens but stem elongation decreases dry mass of many species.

Ultraviolet light responses range from detrimental to beneficial among plant species and have been shown to alter secondary metabolism.

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