



Employing complementary light spectra represents a novel approach for investigating the enhancement of plant resilience in stressful conditions

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ABSTRACT

The aim of this study was to explore how various spectra of complementary light impact the growth and development of strawberry plants under stress conditions caused by salinity and alkalinity. The experiment involved cultivating plants in a greenhouse with ambient light, subjecting them to blue (460 nm), red (660 nm), blue/red (1:3), and white/yellow (400-700 nm) light at different developmental stages. Stress treatments included control (without stress), alkalinity (40 mM NaHCO₃), and salinity (80 mM NaCl). Results indicated a decrease in dry weights under salinity and alkalinity stress. The blue and red spectra were more effective in mitigating stress effects compared to other spectra. While stress conditions led to a reduction in SPAD, blue light increased SPAD under stress. Stress conditions decreased RWC, and blue/red light increased RWC under stress conditions. Blue/red and white/yellow light had the most significant impact on reproductive traits. Salinity and alkalinity stress reduced OJIP curves compared to the control, but the blue and red spectra increased OJIP curves under their respective stress conditions. In conclusion, manipulating the supplemental light spectrum can alleviate the effects of salinity and alkalinity stresses, suggesting the potential extension of artificial light use in stress conditions.

ARTICLE

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1. Introduction

Abiotic stresses pose a significant challenge to crop production and food security as they disrupt the growth, physiology, and function of plants (Wang et al., 2016). Efforts have consistently been made to mitigate these stress effects on plants, and one potential avenue is the utilization of various spectra of complementary light. The interaction of environmental and internal factors controls plant growth, with light quality being a crucial factor dependent on the composition and effective wavelengths in photosynthesis, thereby influencing plant development (Patil et al., 2001). Light, as a fundamental energy source, plays a vital role in plant growth, flowering, fruiting, and photosynthesis (Cho et al., 2008). Water relations of plants change under stress conditions (Lu and Fricke, 2023). A decrease in the relative water content of the leaf indicates a lower turgor, which is caused by the limitation of water availability for the growth and development of leaf cells (Dos Santos et al., 2022). Accumulation of salt in the root area by reducing the osmotic potential prevents water absorption by the roots and thus reduces the water content of the leaf. Under alkalinity stress, water content decreases due to the harmful effect of high pH on plant roots and water absorption or solute accumulation (Yang et al., 2008a). It has been shown that under the influence of salinity and alkalinity, the relative amount of leaf water decreases (Sai Kachout et al., 2011).

Photosynthesis in plants is a complex process that involves the absorption of light and its conversion into chemical energy. Chlorophyll fluorescence is a simple and effective way to measure how plants respond to stressful conditions (Borawska-Jarmułowicz et al., 2014). This technique enables the assessment of a plant's status in unfavorable environmental situations by analyzing fluorescence data. The parameters measured are closely linked to the performance of the photosystem II. When a green plant is exposed to stress, which affects photosynthetic metabolism directly or indirectly, the function of chlorophyll fluorescence changes. Since the variable fluorescence of chlorophyll strongly reacts to changes in the activity of photosystem II, fluorescence quenching analysis provides information on energy absorption, utilization, and dissipation, as well as electron transport in photosystem II (Kalaji et al., 2014). Fluorescence reflectance represents the photochemical efficiency of the photosynthetic apparatus and offers useful data on the functional and structural characteristics of the mechanisms engaged in photosynthetic electron transport (Kalaji et al., 2013). Fluorescence quenching analysis provides information on energy absorption, utilization and dissipation, and electron transport in photosystem two (Kalaji et al., 2014). This makes it possible to evaluate the performance of the plant's photosynthetic apparatus and its tolerance to stress conditions (Maxwell and Johnson, 2000). Several studies have demonstrated the ability of the JIP-Test to reveal changes in the photochemistry of photosystem two (caused by environmental or genetic factors). In addition, it has been found that salinity affects the activity of photosystem two and its effects also differ with salinity levels and species used (Dąbrowski et al., 2016).

Numerous studies have explored the impact of different LED light wavelengths on various plants. LED radiation has been shown to affect the nutrients and quality of strawberries (Johkan et al., 2010). The light spectrum significantly influences plant morphology, growth, and development, as observed in the physiological and morphological improvements of lettuce under drought stress with a combination of blue and red lights (Ginzburg and Klein, 2020). Environmental stresses, particularly soil salinity and alkalinity, are global impediments to plant growth in agriculture (Wang et al., 2018). Photosynthesis is the foundation of plant growth, and its quality is determined by factors like leaf growth, photosynthetic carbon absorption, stomatal movement regulation, chloroplast structure, and accumulation of

photosynthetic pigments. Different light spectrums have varying effects on plants depending on the type of plant, organ, and tissue. For instance, blue and red light can cause stomata to open, while green light can cause stomata to close. Blue light can help in the growth of chloroplasts, while a combination of red, blue, and green lights can increase the plant's leaf area. Similarly, red light can increase the accumulation of photosynthesis products. Higher plants and green algae perform the most photosynthesis in the orange and red light spectrum. Blue and violet light results in lower amounts of photosynthesis, while green light leads to the least amount of photosynthesis. Ultraviolet light can reduce the electron transport activity of photosystem II (Zheng et al., 2008).

Past experiments utilizing LED light sources in growth chambers or greenhouses have aimed to enhance plant growth and quality (Nestby and Trandem, 2013). Employing different spectra of light as complementary light in greenhouses may yield positive effects on plants under salinity and alkalinity conditions. Extending these experiments to stress conditions and investigating plant responses to stress under diverse LED light spectra could provide valuable insights. The application of complementary light spectra through light-emitting diodes (LEDs) emerges as a promising approach to enhance plant resilience under stress conditions. Salinity and alkalinity, as prevalent environmental challenges, represent severe threats to agriculture (Sun and Jiang, 2016). The integration of complementary light in greenhouses has the potential to alleviate the detrimental effects of these stresses on greenhouse plants.

The application of LED technology in horticulture can be expanded in various fields. Most experiments are limited to the effect of some light spectra on plant growth and development. These studies can be extended to the effect of different light spectra on plants under stress conditions. Abiotic stresses such as salinity and alkalinity are widespread environmental problems and are the most severe hazards to agriculture (Sun and Jiang, 2016). The use of complementary light in greenhouses may also reduce the adverse effects of these stresses on greenhouse plants. In this experiment, we investigated the effect of salinity and alkalinity stress in Camarosa variety as a commercial variety. Specifically, we aimed to determine whether the use of different complementary light spectra could improve the tolerance of strawberry plants under salinity and alkalinity stress conditions. To achieve this goal, we investigated how complementary light spectra affect parameters such as growth and development and the electron transport chain of the photosynthetic apparatus in strawberry plants under stress conditions. We hypothesize that the use of additional lighting has a positive effect on the functioning of the photosynthetic apparatus of strawberry plants, therefore the selection of the appropriate light spectrum can reduce the adverse effects of salinity and alkalinity stress.

2. Materials and Methods

2.1. Plant material and growth conditions

This experiment was conducted in the Vali-e-Asr University experimental greenhouse in 2021. We prepared rooted strawberry plants (*Fragaria × ananassa* Duch, cv. Camarosa) from a nursery in Karaj, Iran. Plants were planted in a hydroponic system in a 4-liter pot containing cocopeat and perlite (ratio 70:30 V: V). Each treatment included three pots, and three plants were planted. The plants were growing in a greenhouse with a temperature of 25/15±2°C (day/night), 13/11 h (light/dark) photoperiod, relative humidity of 50±10%, and maximum light intensity above the canopy per day 1085 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (LED+ambient light). The plants were irrigated with Morgan nutrient solution (Morgan, 2003) (EC: 1.4 dS $\cdot\text{m}^{-1}$, pH: 6.5) (Table 1). Plants were treated by five different light conditions (light spectrum). The spectral ranges included monochromatic blue (with a peak at 460 nm), monochromatic red

(with a peak at 660 nm), dichromatic blue/red (at a ratio of 1:3), white (covering the range of 400 to 700 nm) as well as a control group with no LED treatment. Three stress levels, including control (non-stress), alkalinity (40 mM NaHCO₃), and salinity (80 mM NaCl). Plants cultivated under metal structures (length: 100 cm, width: 5cm, and height: 5 cm) With LED tubes with 24W of power and photon flux density (PPFD) of 200 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (Parto Roshd Novin Company, Iran grow light, Iran). Directly above each of the plants, LED lighting systems were mounted 30 cm apart, and the illumination intensities of the LEDs were maintained at 200 $\mu\text{mol m}^{-2} \text{s}^{-1}$ at the leaf surface. LED+ambient light received by plants had a photon flux density of 1085 $\mu\text{mol m}^{-2} \text{s}^{-1}$.

2.2. Vegetative and Reproductive growth characteristics

At the end of the study (60 days after planting), plants were collected for assessment. The branches, roots, and crowns were meticulously separated, and the individual samples were weighed to obtain their fresh weight. Subsequently, to determine the dry weight, the samples were subjected to an oven at 70 °C for 72 hours, and the resulting dry weight was recorded. Leaf area measurements were conducted by randomly selecting three-leaf samples from each treatment and utilizing a 202 m-CI leaf area meter. The early yield and the count of inflorescences were documented throughout the plant's growth period.

2.3. SPAD values and RWC

The chlorophyll index of young leaves was documented using a SPAD-502 Chlorophyll Meter manufactured by Minolta Camera Co. Ltd., Osaka, Japan.

Fresh leaves were used to determine the relative RWC. One leaf from the fully expanded leaf was cut from each plant. Leaf disks (5 mm diameter) were obtained from the leaves. To determine the fresh weight (FW), the prepared leaf discs were weighed. Then, it floated on distilled water in a petri dish and incubated under normal room temperature. After four hours, the adhering water of the discs was blotted and then weighed to determine turgor weight (TW). The samples were dried at 70 ° C for 24 h, and the dry weight (DW) was obtained (Pask et al., 2012). Relative water content was calculated using the following equation:

$$(\text{RWC in \%}) = [(\text{FW} - \text{DW})/(\text{TW} - \text{DW})] \times 100.$$

FW: Fresh weight, DW: dry weight, TW: turgor weight.

2.4. Prompt Chlorophyll a Fluorescence

The chlorophyll fluorescence parameters were assessed using a portable photosynthetic analyzer 60 days post-planting (PEA, Hansatech Instruments, King's Lynn, UK).

2.5. Experimental design and data analysis

This experiment was performed as a completely randomized design with two factors in three replications as a factorial, each consisting of three individual plants in pots. Data analysis was conducted using SAS software version 9.4 from SAS Institute in Cary, NC, USA. The statistical assessment involved a two-way ANOVA model. Upon identifying significant treatment effects in the analysis of variance (ANOVA), the multiple ranges Duncan test was applied as a post hoc to calculate significant mean differences ($P < 0.05$). Subsequently, post hoc range tests and pairwise multiple comparisons were utilized to

determine distinct subsets of means that did not significantly differ from each other. Graphs were drawn using Microsoft Excel (2016).

3. Results

3.1. Vegetative and reproductive characteristics

The results showed that light, stress and their interaction had significant effects on vegetative traits. Salinity and alkalinity stress caused significant reduction in dry weight of leaves, crowns and roots under all light conditions. At salinity stress, the lowest dry weight loss of leaves, crown and roots compared to the without stress was obtained in the blue spectrum. In alkaline stress, the lowest reduction of leaf and crown dry was obtained compared to the without stress in the red spectrum. The highest number of inflorescences and fruits was obtained in blue/red light treatment and control. Under salinity and alkalinity stress conditions, the highest early yield was observed in red and white/yellow light, respectively (Table 1).

3.2. SPAD values and RWC

As per the outcomes depicted in Figure 1, both light and stress exerted a noteworthy influence on the SPAD index and relative water content. The findings indicated that the SPAD index reached its peak under white/yellow, blue/red, and red light, but diminished under conditions of salt and alkalinity stress. Specifically, complementary blue light, when combined with ambient light during salt stress, resulted in an increased SPAD index compared to the control. Conversely, for other light spectrums, the SPAD index experienced a decline under stress conditions. The lowest SPAD index was observed under alkaline stress, and the various light treatments did not exhibit significant differences (Figure 1A). Complementary light spectra demonstrated the capacity to enhance relative water content (RWC) under stress conditions as opposed to the control. Red and blue/red light yielded the highest RWC under salinity stress, while other complementary light spectra showed no significant variation. In the context of alkaline stress, blue/red light exhibited the most pronounced impact on RWC, whereas ambient light resulted in the lowest RWC (Figure 1B).

3.3. Prompt Chlorophyll a Fluorescence

Both, salinity and alkalinity stress significantly decreased the fluorescent transients compared to non-stresses plants in all light treatments, especially at the I and P steps. However, different light spectra reduced the stress effects and increased the fluorescent transients compared to the treatment without supplementary light. Under salt stress, the higher course in all points has the curve in plants with addition of blue light. In I and P points also addition of red light caused positively changes. The positively changes under alkalinity stress were only in I and P points and they were caused by red, blue/red and white/yellow light (Fig 2).

4. Discussion

The first response of plants to salinity stress involves limiting leaf area and experiencing reduced growth (Parida and Das, 2005). The decline in strawberry yield under salinity stress is attributed to a decrease in both the quantity and weight of fruits. Additionally, salt stress induces leaf chlorosis, diminishes leaf area, and lowers photosynthesis due to chlorophyll degradation (Saied et al., 2005).

Table 1 Interaction of light sources and stress on vegetative and reproductive characteristics and SPAD of strawberry cv. Camarosa

Light sources	Stress	Leaf dry weight (g.plant ⁻¹)	Crown dry weight (g.plant ⁻¹)	Root dry weight (g.plant ⁻¹)	Inflorescence number (Plant ⁻¹)	Early yield (g.plant ⁻¹)
Blue (460 nm)	without stress	6.44 ± 0.11 ^c	1.15 ± 0.11 ^{def}	4.33 ± 0.19 ^{de}	2.11 ± 0.11 ^{cd}	26.2 ± 0.9 ^{gh}
	Salinity	4.77 ± 0.11 ^{de}	1.10 ± 0.11 ^{def}	3.66 ± 0.19 ^f	1.22 ± 0.11 ^g	18.4 ± 1.09 ⁱ
	Alkalinity	2.77 ± 0.29 ^{gh}	0.64 ± 0.10 ⁱ	2.00 ± 0.19 ^g	1.22 ± 0.11 ^g	25.6 ± 0.33 ^{gh}
Red (660 nm)	without stress	8.22 ± 0.67 ^b	1.52 ± 0.04 ^c	4.66 ± 0.38 ^d	2.66 ± 0.19 ^b	48.0 ± 1.64 ^c
	Salinity	4.66 ± 0.19 ^{de}	1.04 ± 0.07 ^{efg}	3.88 ± 0.29 ^{ef}	1.66 ± 0.19 ^{ef}	31.4 ± 2.37 ^e
	Alkalinity	4.33 ± 0.50 ^{def}	1.07 ± 0.05 ^{d-g}	2.33 ± 0.02 ^g	1.44 ± 0.11 ^{fg}	25.2 ± 2.47 ^h
Blue/Red (1;3)	without stress	10.30 ± 1.15 ^a	1.82 ± 0.07 ^b	6.44 ± 0.29 ^b	3.77 ± 0.11 ^a	68.2 ± 1.72 ^b
	Salinity	4.33 ± 0.19 ^{def}	0.94 ± 0.13 ^{fgh}	4.77 ± 0.11 ^{cd}	2.44 ± 0.11 ^{bc}	29.6 ± 0.88 ^{efg}
	Alkalinity	2.55 ± 0.29 ^h	0.85 ± 0.06 ^{ghi}	2.33 ± 0.19 ^g	1.55 ± 0.11 ^{efg}	9.44 ± 0.601 ^j
White/ yellow (400-700 nm)	without stress	10.20 ± 0.40 ^a	2.28 ± 0.03 ^a	8.77 ± 0.22 ^a	1.77 ± 0.11 ^{def}	108.0 ± 1.07 ^a
	Salinity	5.55 ± 0.40 ^{cd}	1.21 ± 0.03 ^{de}	5.33 ± 0.19 ^c	1.88 ± 0.11 ^{de}	30.3 ± 1.20 ^{ef}
	Alkalinity	4.00 ± 0.50 ^{efg}	1.15 ± 0.04 ^{def}	3.44 ± 0.11 ^f	1.44 ± 0.11 ^{fg}	39.5 ± 2.37 ^d
Ambient light	without stress	8.00 ± 0.69 ^b	1.29 ± 0.07 ^d	8.33 ± 0.19 ^a	1.55 ± 0.11 ^{fg}	27.1 ± 1.63 ^{e-h}
	Salinity	3.22 ± 0.29 ^{fgh}	0.75 ± 0.05 ^{hi}	3.55 ± 0.29 ^f	1.44 ± 0.22 ^{fg}	14.1 ± 0.86 ⁱ
	Alkalinity	1.88 ± 0.40 ^h	0.69 ± 0.05 ⁱ	2.55 ± 0.22 ^g	1.44 ± 0.11 ^{fg}	17.5 ± 1.44 ⁱ
Significance	Light (L)	***	***	***	***	***
	Stress (S)	***	***	***	***	***
	L × S	**	***	***	***	***

Values are means ± SE of three replicates. Bars with different letters show significant differences at $P \leq 0.05$ (Duncan).

Significance according to ANOVA, ns, *, **, ***, no significant and significant $P \leq 0.05$, 0.01, 0.001, respectively.

Control (no stress), salinity (80 mM NaCl) and alkalinity (40 mM NaHCO₃).

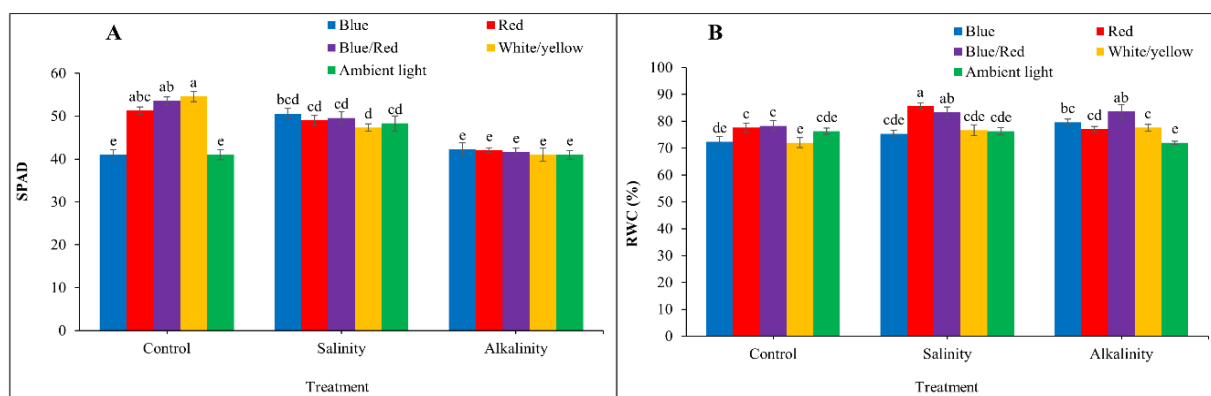


Figure 1 Variations in the SPAD index (A) and RWC index (B) were observed in strawberries of the Camarosa variety, subjected to five levels of light spectrum and three stress levels, with three repetitions. Parameters sharing the same letter indicate no significant differences according to the Duncan test ($p \leq 0.05$). The vertical bars represent standard errors across three replicates. Data analysis was performed using SAS software version 9.4.

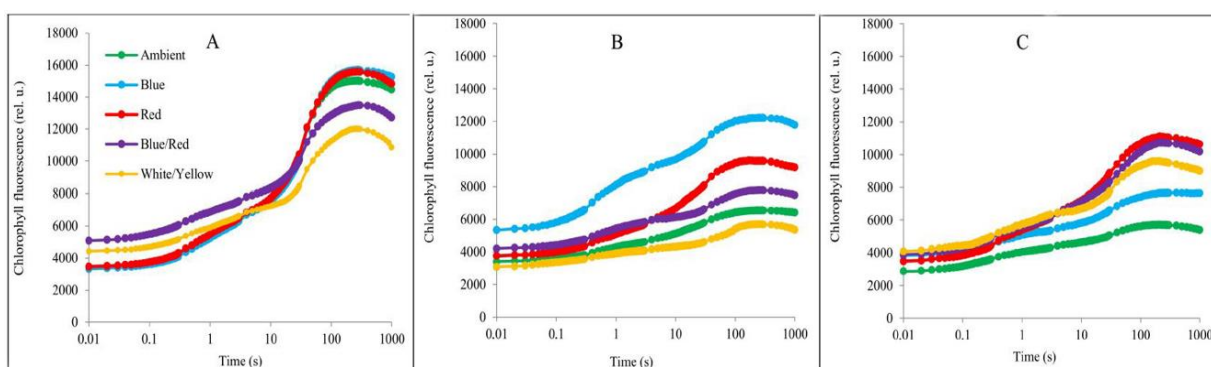


Figure 2 Induction curves of chlorophyll a fluorescence of strawberry cv. Camarosa grown under stress conditions and different light spectra. A: control conditions (without stress); B: salt stress; C: alkalinity stress.

Plants possess the ability to perceive alterations in light quality through light receptors, regulating their growth and development via signaling pathways. It is well established that the morphological, physiological, and nutritional attributes of plants are influenced by the quality and intensity of light (Ward, 2008).

Chloroplasts predominantly absorb blue and red light for photosynthesis (Buschmann et al., 2000). Our investigation focused on the impact of specific light spectra as supplemental light on the vegetative and reproductive processes of strawberry cv. Camarosa. Certain light spectra have been demonstrated to enhance plant resistance to both biological and abiotic stresses (Kreslavski et al., 2013). Our findings revealed that blue and red light, particularly blue light, exerted a more pronounced effect on vegetative traits and demonstrated a greater capacity to alleviate stress compared to other light spectra. Blue light plays a crucial role in chlorophyll biosynthesis, and various studies have highlighted the significance of the combination of blue and red spectra in influencing leaf area and plant biomass (Stutte et al., 2009; Johkan et al., 2010).

Evidence suggests that light quality can impact fruit size (Díaz-Galián et al., 2021). In previous studies, the application of a combination of blue and red light significantly increased fruit production (Choi et al., 2015). Wang et al. (2016) reported an increase in shoot dry

weight under blue/red light, emphasizing that blue and red light enhances plant resilience to stress conditions by influencing photosynthetic efficiency. Moreover, blue light has been shown to stimulate pigment biosynthesis (Taulavuori et al., 2017).

5. Conclusions

Analysis of the vegetative and reproductive characteristics of strawberry plants reveals that plants employ varied strategies in response to abiotic stress contingent on the quality of light. The findings indicate that blue and red-light spectra impact the absorption of elements and the photosynthetic apparatus in plants, thereby enhancing both vegetative and reproductive growth while bolstering the plant's resistance to stress. While white/yellow light enhances the vegetative traits of strawberry plants under non-stress conditions, plants exposed to additional blue, red, and particularly the combination of blue and red light demonstrate improved tolerance to stress conditions. The performance of the photosynthetic apparatus is influenced by light spectra, affecting plant resistance to stress conditions. A comprehension of the impacts of these spectra in diverse growth conditions lays the groundwork for manipulating light spectra to enhance plant resilience to stress. While LED technology holds promise for greenhouse plants, further research is required to thoroughly investigate the effects of LEDs on various plant species and under different environmental conditions.

Conflict of interest

The authors declare no conflict of interest.

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