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# Enhanced Salt Tolerance of Pea (*Pisum sativum* L.) Seedlings Illuminated by LED Red Light

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**Abstract:** Light quality is an important variable affecting plant growth, so we aimed to explore the impact of light quality on plants under salt stress. The salt tolerance of pea (*Pisum sativum* L.) seedlings illuminated by LED red light and 4:1 of red/blue light in a hydroponic system was evaluated at three salinity levels (0, 50, and 100 mmol/L of NaCl) for their morphological and physiological parameters and their root growth characteristics in response to salt stress. Results demonstrated that, as salt stress intensified, the plant height, aboveground fresh/dry mass, root growth indices, and chlorophyll content of pea seedlings exhibited a decreasing trend, while the malondialdehyde (MDA) content and the activity of superoxide dismutase (SOD), peroxidase (POD), and catalase (CAT) in leaves increased. Also, more sodium ($Na^+$) but less potassium ($K^+$) ions were detected due to the change in electrolyte balance. Compared with pea seedlings under no salt stress, the growth rate, plant height, and $K^+$ ion content significantly increased with the red light treatments, but both lights did not affect the aboveground fresh/dry mass, chlorophyll content, or root growth index. Under medium salt stress (50 mmol/L), red light helped generate more chlorophylls by 17.06%, accelerate leaf electrolyte exudation by 23.84%, accumulate more $K^+$ ions by 46.32%, and increase the $K^+/Na^+$ ratio by 45.45%. When pea seedlings were stressed by 100 mmol/L salinity stress, red light was able to maintain the leaf chlorophyll level by 114.66%, POD enzyme activity by 157.78%, MDA amount by 14.16%, leaf and stem electrolyte leakage rate by 38.76% and 21.80%, respectively, $K^+$ ion content by 45.47%, and $K^+/Na^+$ ratio by 69.70%. In conclusion, the use of red light has proven to enhance the salt tolerance of pea seedlings in a hydroponic system, which can and should be a promising approach to prime pea seedlings for more salt tolerance.

**Keywords:** pea; LED red light; salt stress; physiological responses; growth indicators



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## 1. Introduction

Salt stress is one of the most important factors inhibiting plant growth [1]. Seed germination and the seedling stage are the periods most sensitive to soil salinity. If plant salt stress occurs at these early and vulnerable stages, the entire growth and later development

can be severely hindered [2]. Understanding mechanisms involved in crop salt tolerance is of great importance and can lead to finding ways to enhance crop tolerance against salt stress in modern agricultural production. Many attempted, endeavoring, and encouraging approaches in this area include breeding for salt-tolerant varieties [3], adversity exercises (including cross-adaptation) [4,5], use of exogenous substances [6], and lighting modulation and priming [7]. Among these, the approach of adjusting light quality is a novel technology to change physiological responses or adjust key metabolisms for enhanced salt tolerance in crops, having the advantage of being fast, safe, and without limitation by various development stages, and therefore has become one of the most researched fields.

Light quality refers to the composition of light wavelengths and their proportions. It can be divided into ultraviolet light, visible light, and infrared light. Among them, the two kinds of light that have the most important influence on plant photosynthesis are blue light (with a wavelength of 450–495 nm) and red light (with a wavelength of 620–760 nm) in visible light. Plants perceive changes in light quality through photoreceptors and adapt to a series of environmental conditions. For example, blue light is mainly absorbed by phototropin and cryptochrome, affecting plant photosynthesis, phototropism, and photoperiodism. Red light is mainly absorbed by phytochrome, influencing seed germination and flowering, along with seedling morphogenesis and photosynthesis [8]. Goins et al. [9] found that red LED light caused less main stem development but longer main stem length during wheat vegetative growth than white light, while red LED light supplemented with some blue light helped produce larger plants and more grains at harvest. Liu et al. [10] treated 'Miaoxiang 7' strawberry with red light and found enhanced photosynthesis in the leaves and high soluble solids and vitamin C in the fruits. Li et al. [11] found that red/blue (3:1) light proved to significantly increase the net photosynthetic rate, gas exchange, photosynthetic electron transfer capacity, photochemical efficiency, and aboveground and root biomass accumulation in pepper seedlings compared with white light. Chrysanthemums exposed to blue and far red light demonstrated a longer internode length than those exposed to red light [12], probably due to the fact that red light significantly affects photosynthesis through generating more chlorophylls but simultaneously inhibiting carbohydrates from moving out of source organs, specifically leaves [13,14]. In the context of physiological development, the application of red light promoted cell division and elongation, along with stem elongation [14,15]. Cultivated lily plants under exposure to a high percentage of red (80%) and blue light (20%) as background have been used as an effective way to promote extensive stem elongation [16]. While red light positively enhanced the $K^+$ uptake in cucumber and spinach [17,18], blue light hindered it. However, blue light enhanced the $K^+$ uptake in leek and garlic [19].

Under salt stress, different red/blue light ratios have been reported to affect gene expressions such as VvLhcs and light harvesting chlorophyll genes found in *Vitis vinifera* [19] and increase the aboveground biomass of lettuce. When red light is combined with blue, the bluer wavelength usually reduces lettuce plant growth, but, compared with dichromatic light, both blue and red light increases leaf size and epidermal cell area but reduces root dry mass, SPAD index, stomatal density, and leaf thickness [20]. In addition, changes in the ratio of red/far-red light can affect plant salt resistance by modulating the production of different physiological metabolites in plants [19,20]. Moreover, a pretreatment of red light has proven to promote the activity of antioxidant enzymes, accumulation of the biomass in healing tissues, and UV-A tolerance in lettuce photosynthetic cells [21–25]. In summary, red light plays an important role in plant growth and development, photosynthesis, maturation and senescence, fruit quality, and plant resistance to various stresses.

Legumes are economically important crops and pea sprouts are favored by consumers as fresh for their nutritional value and health benefits [26]. No study has been reported

on the salt tolerance of pea sprouts or seedlings through modulating lighting quality. Therefore, the aim of this experiment was to investigate the effect of LED red light on pea salt tolerance at its germination and seedling stages in a hydroponic system through investigating its growth and physiological parameters. The effect of red light on the salt tolerance of pea seedlings may shade some light on the potential impact of red light on the salt tolerance of mature pea plants or other field crops.

## 2. Results and Analyses

### *2.1. Effect of Salt Stress on Seed Germination*

The germination rate of pea seeds with all treatments increased during the 3-day assessment. However, a higher salinity level seemed to hinder seed germination in the first two days, while there was no difference in the seed germination rate on the third day (Figure 1). Compared with CK, the germination rate of pea seeds with the 50 mmol/L and 100 mmol/L salt treatments was 31.1% and 48.7% on day 1, and 8.8% and 33.9% on day 2 post sowing, respectively. There was no significant difference in the germination rate between treatments (99.7%, 97.6%, and 96.0% respectively) on day 3 post sowing, suggesting that high salinity up to a 100 mmol/L level delayed seed germination but did not reduce the final germination rate in 3 days.

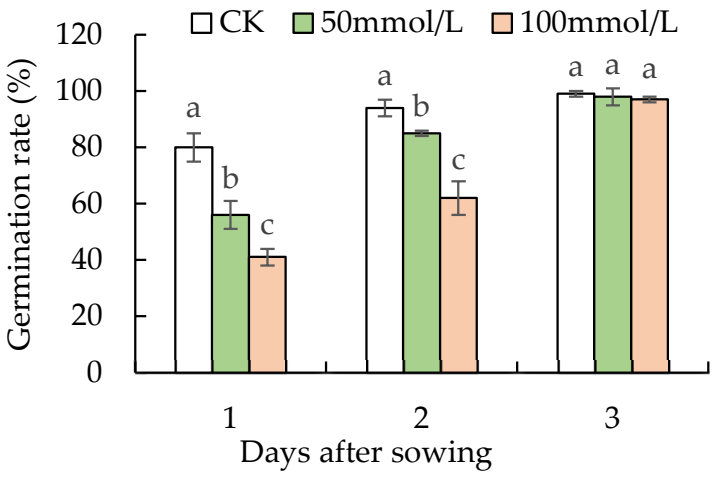


**Figure 1.** Seedling emergence under different concentrations of salt solutions. Different lowercase letters represent differences between treatments on the same day at the 0.05 level of significance.

### *2.2. Effect of Red Light on Aboveground Mass of Pea under Salt Stress*

In the first 6 days after seed germination, under the same light conditions, the plant height of seedlings with the F1, F2, R1, and R2 treatments decreased by 42.82%, 58.42%, 36.57%, and 40.08%, respectively, compared with their corresponding F0 or R0 treatments (Figures 2 and 3a). Twelve days after seed germination, the plant height of these seedlings with the F1, F2, R1, and R2 treatments decreased by 67.09%, 78.14%, 50.86%, and 57.88%, respectively, compared with their CKs (F0 and R0). For the same salinity levels, the plant height of seedlings with the R0 treatment increased by 26.47% and 15.15% in 6 and 12 days after seed germination, respectively, compared with that of seedlings with the F0 treatment. There was no significant difference in the plant height of seedlings between the R1 and F1 treatments 6 days after germination. However, 12 days after seed germination, the plant height of seedlings with the R1 treatment increased by 47.73% compared with those with the F1 treatment. Also, at 6 and 12 days after seed germination, the plant height of seedlings with the R2 treatment increased by 34.62% and 93.75%, respectively, compared with that of the seedlings with the F2 treatment. Evidently, red light enhances the growth of pea seedlings whether there is salt stress or not compared with the control.

As shown in Figure 3b, the aboveground fresh mass of seedlings with the F1, F2, R1, and R2 treatments was 54.21%, 77.22%, 51.11%, and 60.79% lower than that of seedlings with the F0 or R0 treatment, respectively, under the same light conditions 6 days after seed germination. Twelve days after seed germination, the aboveground fresh mass of seedlings with the F1, F2, R1, and R2 treatments was 61.83%, 75.47%, 51.33%, and 52.12% lower than that of seedlings with the F0 or R0 treatment, respectively. For the same salinity levels, there was no significant difference in the aboveground fresh mass of seedlings between the R0 and F0 treatment at both 6 and 12 days after seed germination. However, the aboveground fresh mass of seedlings with the R1 treatment increased by 33.70% and 24.37%, respectively, compared with that of seedlings with the F1 treatment. And the aboveground fresh mass of seedlings with the R2 treatment increased by 15.91% and 56.70%, respectively, compared with that of seedlings with the F2 treatment. It was evident that, in the absence of salt stress, red light did not change the aboveground fresh mass. But, when pea seedlings were under salt stress, the redlight treatment was more effective than red/blue light in increasing the aboveground fresh mass of pea seedlings.

Under the same light conditions, the aboveground dry mass of pea seedlings with the F1, F2, R1, and R2 treatments decreased by 49.32%, 72.97%, 50.00%, and 64.56%, respectively, 6 days after seed germination compared with that of seedlings with their respective F0 or R0 treatments. Twelve days after germination, the aboveground dry mass of F1 and F2 treatments decreased by 60.26% and 75.17%, respectively, and that of R1 and R2 treatments decreased by 43.70% and 49.61%, respectively, compared with that of F0 (Figure 3c). Also, at 12 days after germination, the aboveground dry mass of F1 and F2 treatments decreased by 60.26% and 75.17%, and that of R1 and R2 treatments decreased by 43.70% and 49.61%, respectively, compared with that of R0 treatment. For the same salinity levels, there was no significant difference in aboveground dry mass between R0 and F0 and R1 and F1 treatments at 6 days and 12 days after germination. However, at 12 days after germination, the aboveground dry mass of R2 treatment was 70.67% higher than that of F2, which was a significant increase. It can be seen that, under no/low salt stress, red light did not affect aboveground dry mass in the same way as the control, but, under high salt stress, red light treatment promoted an increase in aboveground dry mass in comparison with the control.

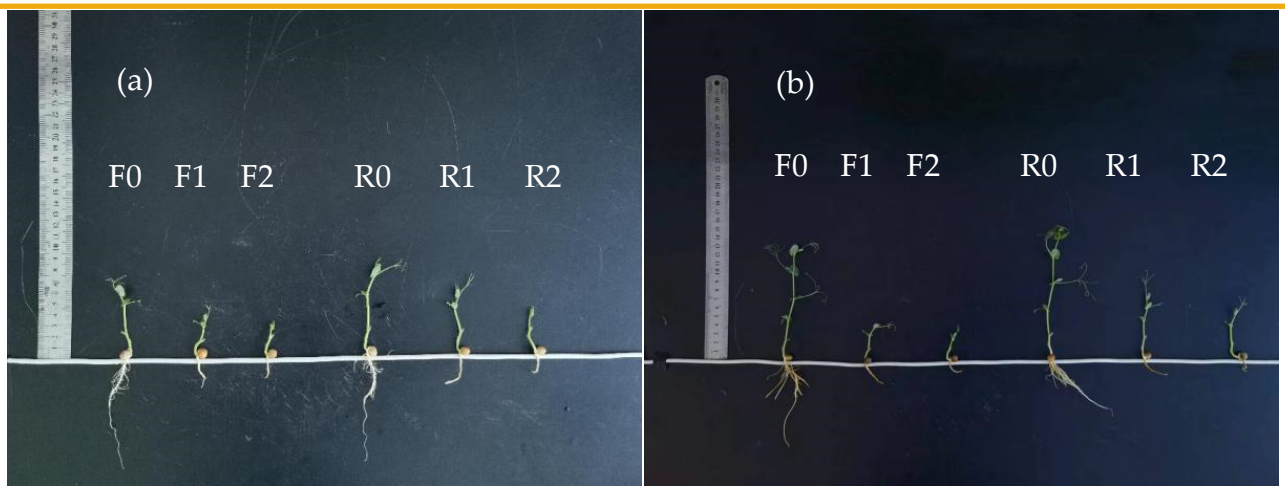


**Figure 2.** Growth of pea seedlings under different light quality and salt stress at 6 days after germination (**a**) and 12 days after germination (**b**).

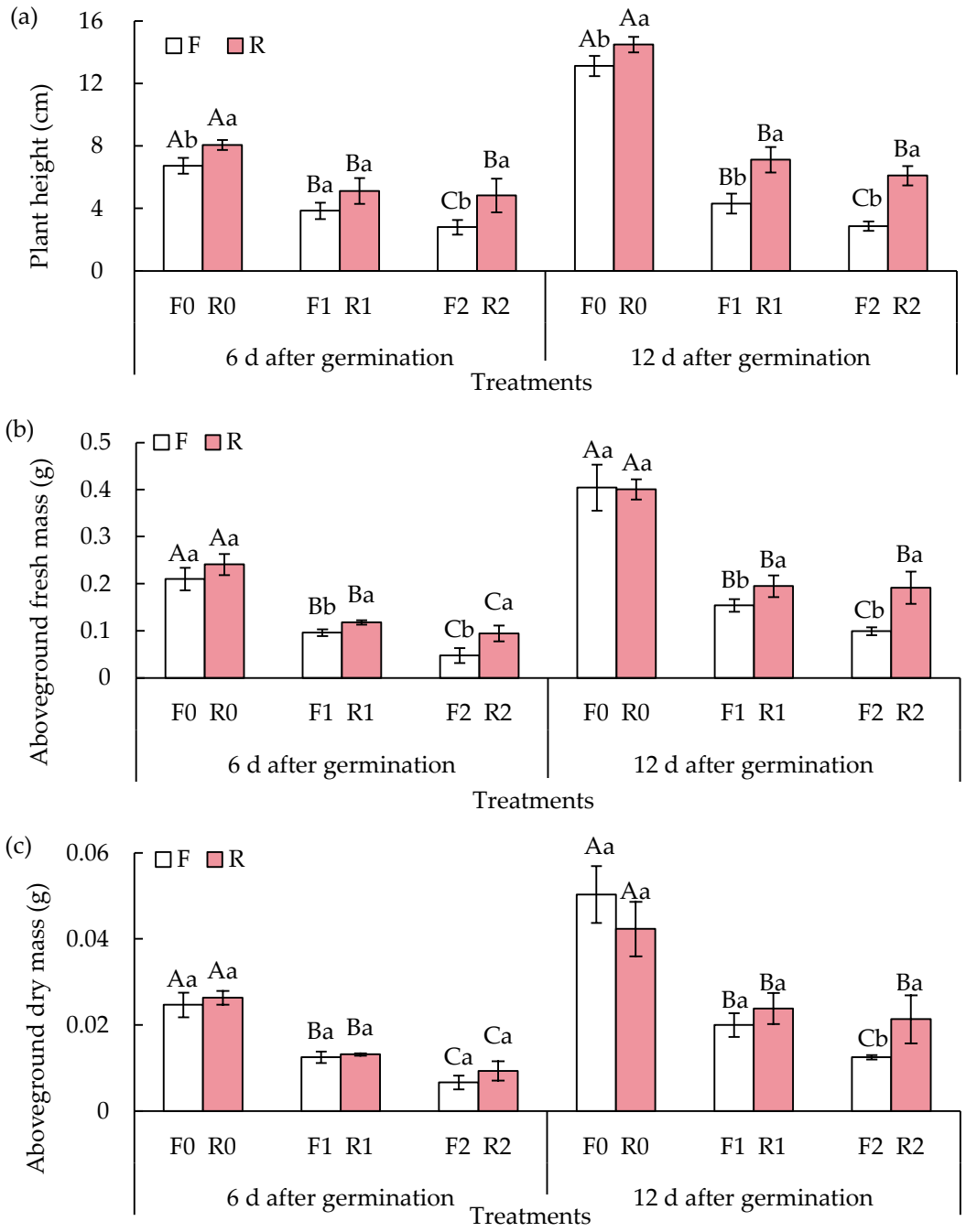


**Figure 3.** Evaluation of aboveground growth of pea seedlings: (**a**) plant height, (**b**) aboveground fresh mass, (**c**) aboveground dry mass with different treatments. Different uppercase letters indicate significant differences in different salt concentrations of the same light quality ($p < 0.05$), and different lowercase letters indicate significant differences in different light qualities of the same salt concentration ($p < 0.05$).

### *2.3. Effect of Red Light on Root Growth of Pea Seedlings Under Salt Stress*

Table 1 presents the total root length (cm), total root surface area ($cm^2$), total root volume ($cm^3$), average root diameter (mm), and root fresh/dry weight (g) of pea. For the total root length, under the same light quality, at 6 d after germination, it was reduced by 84.35% and 85.00% in F1 and F2 treatments compared with F0 treatment, respectively, and was reduced by 73.09% and 82.01% in R1 and R2 treatments compared with R0 treatment, respectively. At 12 d after germination, the total root length in F1 and F2 treatments was 88.08% and 89.11% lower compared with F0 treatment, respectively, while that of R1 and R2

treatments was reduced by 81.48% and 87.85% compared with R0 treatment, respectively. Under the same salt treatments, there was no significant difference in total root length between R0 and F0 treatments at 6 d and 12 d after germination. However, the total root length of R1 treatment increased significantly by 57.66% and 65.53% over F1 treatment at 6 d and 12 d after germination, respectively, and R2 treatment had no significant difference in total root length compared with F2 treatment. This indicates that the redlight treatment favored the increase in total root length to some extent under light salt stress compared with the control.

**Table 1.** Comparison of growth parameters of pea roots on different days between various light and salinity treatments.

| Days After Sowing (d) | Treatments | Total Root Length (cm) | Total Root Surface Area ($cm^2$) | Total Root Volume ($cm^3$) | Average Root Diameter (mm) | Root Dry Mass (g) |
|---|---|---|---|---|---|---|
| 6 | F0 | 58.00 ± 12.84 Aa | 9.83 ± 1.21 Aa | 0.134 ± 0.016 Aa | 0.547 ± 0.022 Aa | 0.017 ± 0.002 Ba |
| | F1 | 9.08 ± 0.72 Bb | 1.22 ± 0.15 Bb | 0.013 ± 0.002 Bb | 0.428 ± 0.009 Bb | 0.006 ± 0.001 Ba |
| | F2 | 8.70 ± 0.24 Ba | 1.16 ± 0.12 Bb | 0.012 ± 0.002 Bb | 0.425 ± 0.011 Ba | 0.004 ± 0.001 Cb |
| | R0 | 53.19 ± 14.55 Aa | 8.38 ± 2.45 Aa | 0.105 ± 0.033 Aa | 0.500 ± 0.004 Aa | 0.018 ± 0.002 Aa |
| | R1 | 14.31 ± 2.01 Ba | 2.04 ± 0.34 Ba | 0.023 ± 0.005 Ba | 0.463 ± 0.013 Ba | 0.005 ± 0.001 Ba |
| | R2 | 9.57 ± 0.53 Ba | 1.40 ± 0.05 Ca | 0.017 ± 0.001 Ba | 0.44 ± 0.009 Ba | 0.005 ± 0.001 Ca |
| 12 | F0 | 85.72 ± 7.99 Aa | 15.05 ± 1.38 Aa | 0.210 ± 0.020 Aa | 0.559 ± 0.005 Aa | 0.027 ± 0.003 Aa |
| | F1 | 10.22 ± 0.34 Bb | 1.30 ± 0.19 Bb | 0.013 ± 0.004 Ba | 0.405 ± 0.023 Ba | 0.009 ± 0.001 Ba |
| | F2 | 9.33 ± 0.59 Ba | 1.05 ± 0.14 Ba | 0.010 ± 0.003 Ba | 0.360 ± 0.017 Ca | 0.003 ± 0.001 Ca |
| | R0 | 91.3 ± 19.19 Aa | 15.62 ± 2.9 Aa | 0.213 ± 0.037 Aa | 0.548 ± 0.010 Aa | 0.029 ± 0.001 Aa |
| | R1 | 16.91 ± 2.09 Ba | 1.73 ± 0.13 Ba | 0.014 ± 0.002 Ba | 0.328 ± 0.012 Ba | 0.007 ± 0.001 Ba |
| | R2 | 11.09 ± 0.73 Ca | 1.10 ± 0.15 Ca | 0.009 ± 0.002 Ca | 0.316 ± 0.011 Ba | 0.006 ± 0.001 Ba |

**Note:** Different uppercase letters indicate significant differences in different salt concentrations of the same light quality ($p < 0.05$), and different lowercase letters indicate significant differences in different light qualities of the same salt concentration ($p < 0.05$).

Regarding the total root surface area, under the same light quality, at 6 d after germination, that of F1 and F2 treatments was 87.55% and 88.16% lower than that of the F0 treatment, respectively; that of R1 and R2 treatments was 75.59% and 83.24% lower than that of the R0 treatment, respectively. Under the same salt treatments, there was no significant difference in total root surface area between R0 and F0 treatments at 6 d and 12 d after germination. The total root surface area of R1 treatment increased significantly by 67.11% and 33.29% over F1 treatment at 6 d and 12 d after germination, respectively. At 6 d after germination, the total root surface area of R2 treatment increased by 20.63% compared with F2 treatment, which was a significant increase, but, at 12 d after germination, the difference between R2 and F2 treatments was not significant. It suggests that the red light treatment favored the increase in total root surface area under salt stress compared with the control.

In terms of the total root volume, under the same light quality, at 6 d after germination, the total root volume of F1 and F2 treatments was reduced by 90.13% and 90.71%, respectively, and that of R1 and R2 treatments was reduced by 77.78% and 84.13%, respectively, compared with the R0 treatment. At 12 d after germination, it was reduced by 93.60% and 95.45% in F1 and F2 treatments, respectively, and by 93.38% and 95.88% in R1 and R2 treatments, respectively, compared with F0 treatment. Under the same salt treatment, there was no significant difference in total root volume between the R0 and F0 treatments at 6 d and 12 d after germination. At 6 d after germination, the total root volume of the R1 treatment increased by 76.47% over the F1 treatment, which was a significant increase, while, at 12 d after germination, the differences between R1 and F1 treatments were not significant. At 6 d after germination, the total root volume of R2 treatment increased significantly by 33.93% compared with F2 treatment, and, at 12 d after germination, the difference between R2 and F2 treatments was not significant. It indicates that the red light treatment favored the increase in total root volume under salt stress compared with the control.

Concerning the average root diameter, under the same light quality, at 6 d after germination, the average root diameter of F1 and F2 treatments decreased by 21.80% and 22.29%, respectively, and that of R1 and R2 treatments decreased by 7.27% and 12.01%, respectively, compared with the R0 treatment. At 12 d after germination, the mean root diameters of the F1 and F2 treatments were reduced by 27.51% and 35.56%, respectively, and the mean root diameters of the R1 and R2 treatments were reduced by 40.17% and 42.24%, respectively, compared with the R0 treatment. Under the same salt stress, at 6 d after germination, the average root diameter of R1 increased significantly by 8.26% over that of F1 treatment, while, at 6 d and 12 d after germination, the differences between R0 and F0 and R2 and F2 treatments were not significant. It suggests that the red light treatment under light salt stress favored the increase in mean root diameter to some extent compared with the control.

For the root dry mass, under the same light quality, at 6 d after germination, the root dry mass of the F1 and F2 treatments was reduced by 64.36% and 76.24%, respectively, and that of the R1 and R2 treatments was reduced by 73.58% compared with that of the R0 treatment. At 12 d after germination, the root dry mass of the F1 and F2 treatments was reduced by 67.68 g and 87.80 g, respectively, compared with the F0 treatment, and the root dry mass of the R1 and R2 treatments was reduced by 75.86 g and 79.31 g, respectively, compared with the R0 treatment. At 12 d after germination under the same salt stress, there was no significant difference in root dry mass between R0 and F0 treatments and between R1 and F1 treatments, whereas R2 showed a significant increase of 100.00% in root dry mass over F2. This indicates that prolonged exposure to red light reduces the reduction in the dry mass of pea roots by salt stress compared with the control light under high salt stress.

### *2.4. Effect of Red Light on Chlorophyll Content of Pea Under Salt Stress*

The chlorophyll content of hemp pea under salt stress in the control red and blue light treatments versus the red light treatments is evidently shown in Figure 4. With the same light quality, compared with the F0 treatment, the chlorophyll content of the F1 and F2 treatments was reduced by 34.32% and 69.77%, respectively. Compared with the R0 treatment, the chlorophyll content of the R1 and R2 treatments was reduced by 28.40% and 39.56%, respectively. Under the same salt stress, there was no significant difference in chlorophyll content between the R0 and F0 treatments. The chlorophyll content of the R1 treatment increased by 17.06% over the F1 treatment, and the chlorophyll content of the R2 treatment increased by 114.66% compared with the F2 treatment, with a significant increase. It indicates that the red light treatment promotes the increase in chlorophyll content in hemp pea under salt stress more than the control.

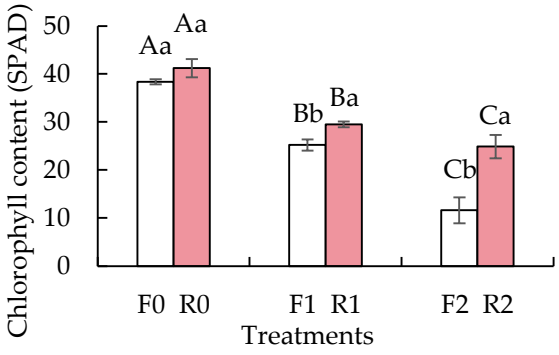


**Figure 4.** The chlorophyll content of pea seedlings between different light and salinity treatments on the 12th day after sowing. Different uppercase letters indicate significant differences in different salt concentrations of the same light quality ($p < 0.05$), and different lowercase letters indicate significant differences in different light qualities of the same salt concentration ($p < 0.05$).

### *2.5. Effect of Red Light on Antioxidant Enzyme Activities of Pea Seedlings Under Salt Stress*

The MDA content and activities of SOD, POD, and CAT enzymes in the leaves of pea seedlings significantly increased with the salinity level in the hydroponic solution (Figure 5). Under the same salinity level, the MDA content in leaves with the R2 treatment was 14.16% less than that in the F2 treatment, but no such significant differences were observed between the R0 and F0 treatments, or between the R1 and F1 treatments. A significantly reduced SOD enzyme activity (by 34.76% and 26.83%) was detected in leaves with the R0 and R2 treatments, but not with R1. The POD enzyme activity significantly increased in leaves with both R1 and R2 treatments (by 73.53% and 157.78%, respectively, $p < 0.05$). There was no significant difference in the CAT enzyme activity in leaves with the two light quality treatments. Since SOD and POD enzymes are relatively sensitive to light quality, the salt-stressed pea seedlings illuminated by red light tended to reduce the MDA content and SOD enzyme activity but increased the POD enzyme activity significantly in comparison with those activities in the F treatments.

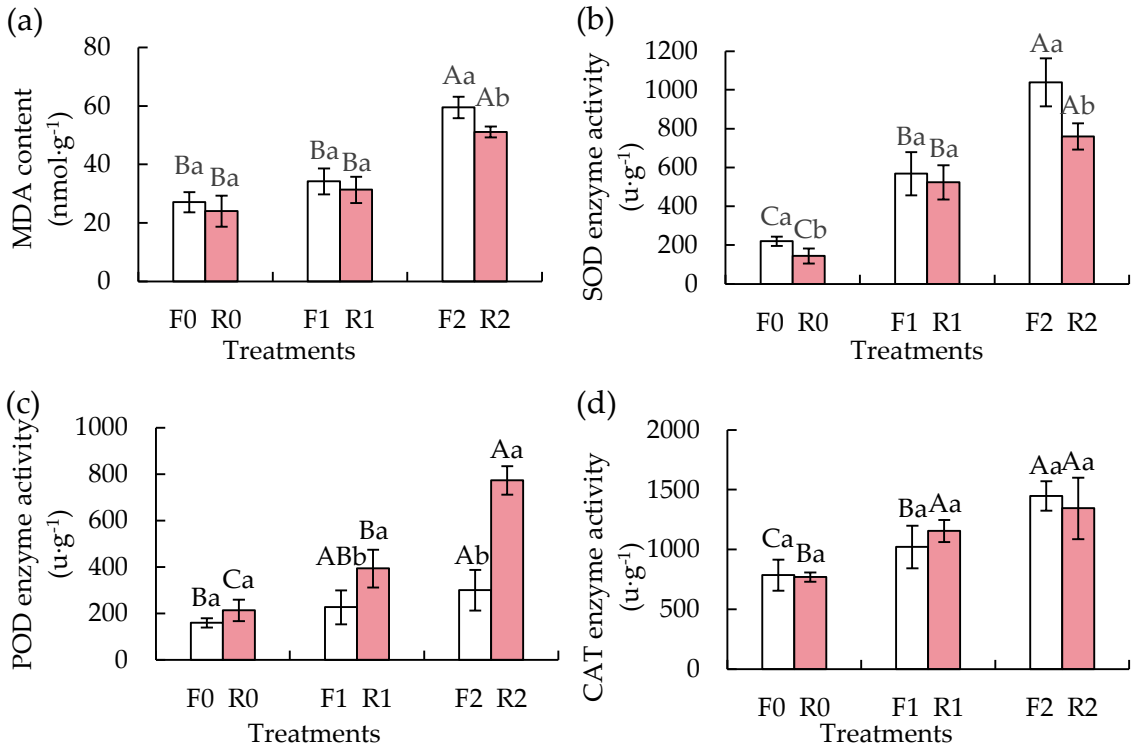


**Figure 5.** Evaluation of antioxidant enzyme activities: (**a**) malondialdehyde (MDA) content, (**b**) superoxide dismutase (SOD) activity, (**c**) peroxidase (POD) activity, and (**d**) catalase (CAT) activity in leaves of pea seedlings between different light and salinity treatments on the 12th day after sowing. Different uppercase letters indicate significant differences in different salt concentrations of the same light quality ($p < 0.05$), and different lowercase letters indicate significant differences in different light qualities of the same salt concentration ($p < 0.05$).

### *2.6. Effect of Red Light on the Electrolyte Leakage Rate in Pea Seedlings Under Salt Stress*

Under the illumination of the same light quality, the leaf electrolyte leakage rate in seedlings with the F1 and F2 (compared with F0) and R1 and R2 (compared with R0) treatments increased by 44.30%, 116.17%, 10.46%, and 33.06%, respectively (Figure 6a). Under the same salinity level, no significant difference in the leaf electrolyte leakage rate was observed between R0 and F0, while a significantly reduced rate of 23.84% in R1 compared with F1 and of 38.76% in R2 compared with F2 was observed. Under the illumination of the same light quality, the stem electrolyte leakage rate in seedlings with

the F1 and F2 (compared with F0) and R1 and R2 (compared with R0) treatments increased by 53.06%, 108.58%, 37.89%, and 36.78%, respectively (Figure 6b). Under the same salinity level, no significant difference in the stem electrolyte leakage rate was observed between the R0 and F0 treatments or between the R1 and F1 treatments, while a significantly lower rate of 21.80% in R2 compared with F2 was observed. Under the illumination of the same light quality, the root electrolyte leakage rate in seedlings with the F1 and R1 treatments did not change significantly compared with their respective F0 and R0 treatments, but increased by 14.24% and 40.57% in roots with the F2 and R2 treatments compared with their respective F0 and R0 treatments (Figure 6c). There was no such significant difference in roots between R0 and F0, R1 and F1, and R2 and F2 treatments under the same salinity levels. Therefore, illumination with red light caused the electrolyte to leak less through the membranes in the leaves and stems of pea seedlings under salt stress.

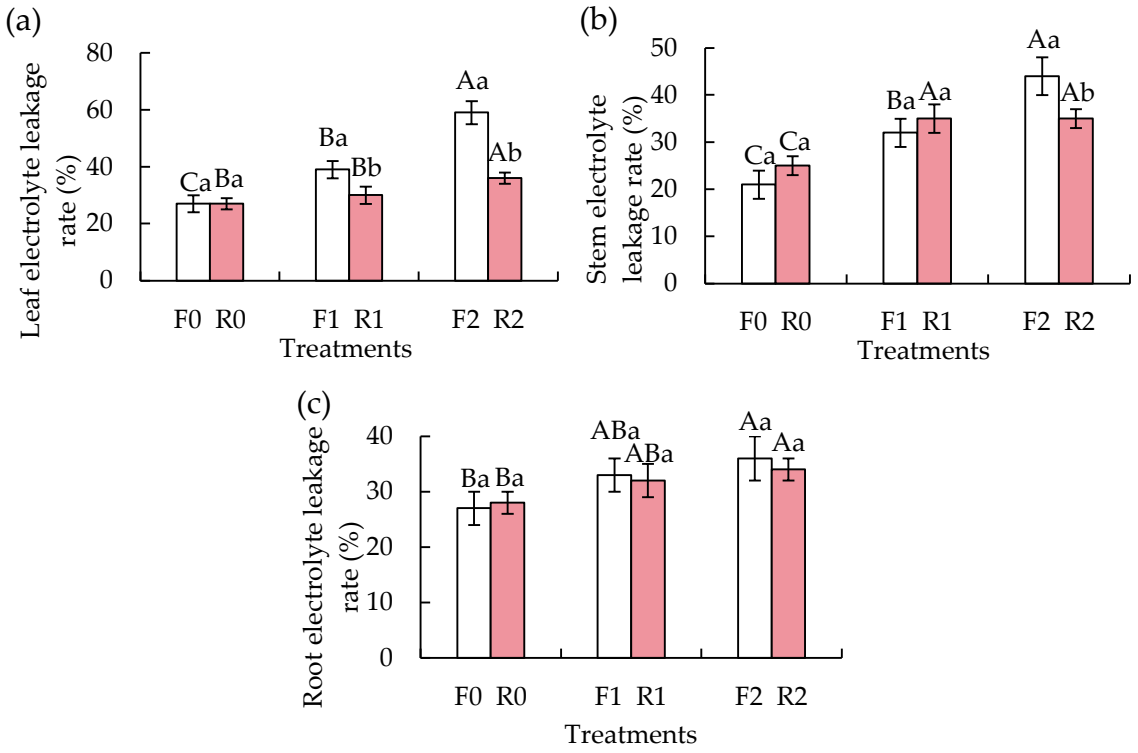


**Figure 6.** The electrolyte leakage rate of different parts of pea seedlings: (**a**) in leaves, (**b**) in stems, and (**c**) in roots between different light and salinity treatments on the 12th day after sowing. Different uppercase letters indicate significant differences in different salt concentrations of the same light quality ($p < 0.05$), and different lowercase letters indicate significant differences in different light qualities of the same salt concentration ($p < 0.05$).

### *2.7. Effect of Red Light on the $K^+$ and $Na^+$ Content and $K^+/Na^+$ Ratio in Pea Seedlings Under Salt Stress*

Under the illumination of the same light quality, the $K^+$ content decreased by 29.99%, 35.48%, 11.09%, and 18.54% in seedlings with the F1 and F2 (compared with F0) and R1 and R2 (compared with R0) treatments, respectively (Figure 7a). Meanwhile, under the same salt stress, the $K^+$ content in seedlings with the R0, R1, and R2 increased significantly by 15.22%, 46.32%, and 45.47%, compared with their respective F0, F1, and F2 treatments, respectively. Under the illumination of the same light quality, the $Na^+$ content in seedlings with the F1, F2, R1, and R2 treatments increased by 1668.39%, 2897.81%, 1889.01%, and 2773.05%, respectively, compared with their respective F0 or R0 treatments (Figure 7b). There was no significant difference in the $Na^+$ content in seedlings when comparing the R0 to F0 and R1 to F1 treatments. However, seedlings with the R2 treatment showed a

significant reduction of 14.28% in the $Na^+$ content compared with the F2 treatment. In terms of the $K^+/Na^+$ ratio, there were significant reductions of 96.04% and 97.85% in seedlings with F1 and F2 (compared with F0), and of 95.53% and 97.16% in seedlings with R1 and R2 (compared with R0) under the illumination of the same light quality (Figure 7c). Meanwhile, there were such significant differences of 28.82%, 45.45%, and 69.70% increases in seedlings when comparing the R0 to F0, R1 to F1, and R2 to F2 treatments, respectively. It was evident that red light increased the $K^+$ content and the $K^+/Na^+$ ratio in pea seedlings with or without salt stress but reduced the $Na^+$ content in seedlings under severe salt stress.

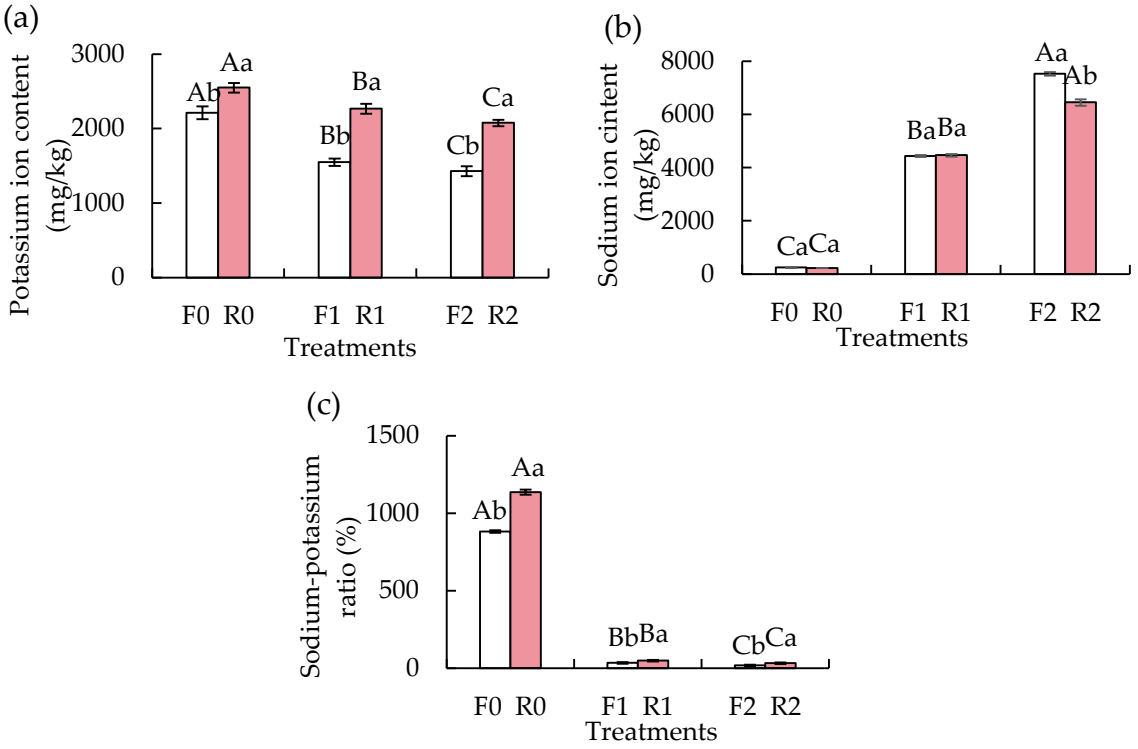


**Figure 7.** Effect of different lights and salinity levels on the $K^+$ (**a**) and $Na^+$ (**b**) content and $K^+/Na^+$ ratio (**c**) of pea seedlings on the 12th day after sowing. Different uppercase letters indicate significant differences in different salt concentrations of the same light quality ($p < 0.05$), and different lowercase letters indicate significant differences in different light qualities of the same salt concentration ($p < 0.05$).

## 3. Discussion

### *3.1. The Impact of Salt Stress on Crops*

Salt stress is an inevitable constraint that the environment imposes on crop production, agricultural development, and ecological conservation, which negatively affects plant growth, development, and reproduction [27]. Our data analysis demonstrated that the process of the pea seed germination was delayed at first under salt stress, but, 3 days after sowing, the final germination rate did not change significantly, suggesting that salt-stressed pea seeds absorbed less water first due to osmotic stress but quickly adjusted to tolerate an unlethal salinity (<100 mmol/L) in their final germination, which was basically consistent with the results reported by Ya et al. [28].

### *3.2. The Role of Light Quality in Plant Growth and Development*

The light environment is crucial for plant growth and development as it influences morphological adjustment, photosynthesis, morphogenesis, root development, metabolisms, photoperiod modulation, and gene expression in plants [29]. Light quality, being one of the

core constituents of the light environment and the most significant technical parameter in supplementary light for facility crops, has always drawn attention. Different wavelengths of light possess different levels of energy, which can impact plant growth and development by modulating photoreceptors, transcription factors, and plant hormones [16,17]. Light quality is capable of affecting the antioxidant capacity of crops, regulating carbon and nitrogen metabolism, and enabling crops to adapt to various abiotic stress environments [18,19]. Among them, red and blue light are most essential in promoting photosynthetic efficiency [30–32]. The illustration of mechanisms involved in sensing quality and intensity of red, blue, or both bended lights by pea seedlings to affect the growth, development, and metabolism is demonstrated in Figure 8.

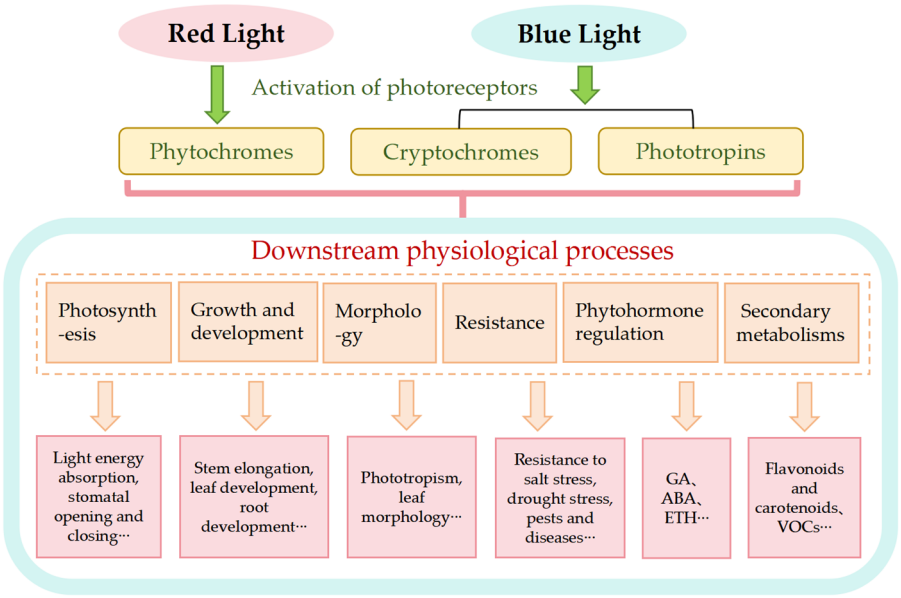


**Figure 8.** The effect of the quality of red and blue lights on the growth, development, and metabolisms of hydroponically cultivated pea seedlings.

In this experiment, red light has proven to be more effective than red/blue (4:1) light in enhancing the growth and height of normal pea seedlings. However, neither of the two lights significantly affected the aboveground fresh/dry mass, chlorophyll content, or root growth indexes, which is basically in agreement with the findings on the effect of red light on tomato growth reported by Mansoori et al. [33]. Under the same salt stress, both growth rate and fresh mass of pea seedlings with the red light treatment were greater than those of seedlings with the red/blue (4:1) light treatment, while the dry matter mass of pea seedlings under the illumination of red light was significantly greater than that of seedlings under the illumination of red/blue (4:1) light treatments only on day 12 with the highest salinity level (100 mmol/L). Red light shows a less inhibitory effect on root growth and development whether under salt stress or not and significantly increases the chlorophyll content of seedlings at different salt stress levels. The difference of growth parameters measured between two different treatments of light quality may be due to the variations of physiological and biochemical levels in response to different light quality acquired by photoreceptors in plants [34,35]. It is generally considered that red light either enhances the tolerance of pea seedlings against salt stress or makes them more sensitive to light quality by promoting the chlorophyll synthesis catalyzed by increased enzyme activities, reducing osmotic damages to cell membranes, improving photosynthetic efficiency, and initiating more dry matter accumulation [7].

### *3.3. The Situation Related to Antioxidant Enzymes*

Abiotic stresses disrupt the balance between ROS production and its elimination, likely resulting in an excessive accumulation of ROS and ultimately leading to oxidative stress [36]. MDA is an oxidative end product of the free radical-induced lipid peroxidation and can indirectly reflect the intensity of oxidative stress [37]. SOD, POD, and CAT are essential antioxidant enzymes that remove excess ROS [38].

Many studies have demonstrated that the activities and efficiencies of antioxidant enzymes in response to abiotic stresses in plants vary depending on the ratio of red to blue light, plant species, genotype, and stages of plant growth and development [39–41]. In this study, all leaves of pea seedlings showed an increasing trend in the SOD, POD, and CAT activities and the MDA content as salt stress intensified. However, the antioxidant enzyme activity demonstrated some variation in seedlings under different lights, in which SOD and POD enzymes showed higher activities and were more responsive to light quality. Under the same salt stress, the SOD activity and MDA content of the red light treatment were lower than those of the seedlings illuminated by red/blue (4:1) light, suggesting that the lack of blue light was unfavorable to increasing the SOD activity, which could be a consequence of lower superoxide production [42,43]. Additionally, the POD activity of pea seedlings illuminated by red light was greater than that of seedlings illuminated by red/blue (4:1) light, which is consistent with the previous findings on the effect of light on antioxidant enzyme activities [44,45]. It is evident that there are certain synergies and antagonisms between various physiological metabolisms in pea seedlings under salt stress. Under illumination by red light, the changes in SOD and POD activities showed an opposite trend, likely due to a delayed signaling transduction in plants or other interfering factors involved in the complexity of the enzymatic activities or diversified responses of plants to oxidative stress and complex regulatory networks [46]. POD and SOD enzyme sensitivity to a certain type of illumination may be due to the fact that light signal pathways can modulate gene expression and secondary signal pathways, adjust synthesis and breakdown of enzymes participating in light-effecting metabolisms, and affect their efficacies [47–51].

### *3.4. The Situation Related to Ionic Balance*

Under NaCl-generated salt stress, the increase in $Na^+$ accumulation and decrease in $K^+$ uptake by plants break the balance of interior ions, causing ionic toxicity and nutrient deficits in plants, and ultimately affecting plant growth and development [52,53]. The results derived from this experiment demonstrated that red light illumination was favorable to the increase in $K^+$ content and decrease in $Na^+$ content, which indicated that a high proportion of red light was required to promote the uptake of $K^+$ by plant cells, reduce the uptake of $Na^+$, and increase the $K^+$-$Na^+$ ratio in order to alleviate the inhibitory effect of ionic imbalance caused by salt stress on the growth of pea seedlings. In addition, salt stress increases the electrolyte leakage rate [54], which can be mitigated by red light illumination on pea seedlings under salt stress, suggesting that red light could alleviate the oxidative damage to cell membranes through reducing the electrolyte leakage rate in pea seedlings.

Light intensity can affect the salt tolerance of crops. When the light intensity is less than 500 μmol/$m^2$/s, it is considered to be relatively low for some plants such as peas [55]. Above that light intensity level, a relatively higher light intensity is conducive to increasing the photosynthetic rate of plants and then alleviating the damage caused by salt stress to plants through various physiological pathways such as increasing the synthesis of osmotic regulatory substances, etc. [56]. Therefore, we believe that the slight difference between the light intensity of the two lamps (390.2 μmol/$m^2$/s and 324.8 μmol/$m^2$/s, respectively) we used did not affect the results at all at such a low intensity. In the future, research on the

optimal combination of light quality and light intensity for improving the salt tolerance of plants should be further explored.

## 4. Materials and Methods

### *4.1. Materials*

Pea seeds were soaked and germinated and their sprouts were planted in 30 cm × 22 cm × 3.5 cm trays and placed on a 4-shelf rack (40 cm high, 100 cm long, and 50 cm wide). Spectra outputs from the various basal lamp/filter combinations were recorded with a calibrated spectroradiometer (LI-COR 1800, Lincoln, NE, USA) placed horizontally in the cabinets used for the experiments, with the sensor covered by the glass lid of the vessel. Different light treatments and salt treatments were carried out at the same time. Four LED light tubes were fixed on the top of each shelf (four lamps per layer) and the whole rack was fully covered with black cloth. The test lighting spectrum was set up with two LED light sources at a 4:1 ratio of red/blue and red light with a photosynthetic active radiation of 390.2 μmol/$m^2$/s and 324.8 μmol/$m^2$/s (T8 36W Grow Light, Beijing Yasheng Zengguang Physical Agricultural Technology Development Co., Ltd., Beijing, China), and the light intensity of 2740 Lx and 2270 Lx, respectively (Figure 9).

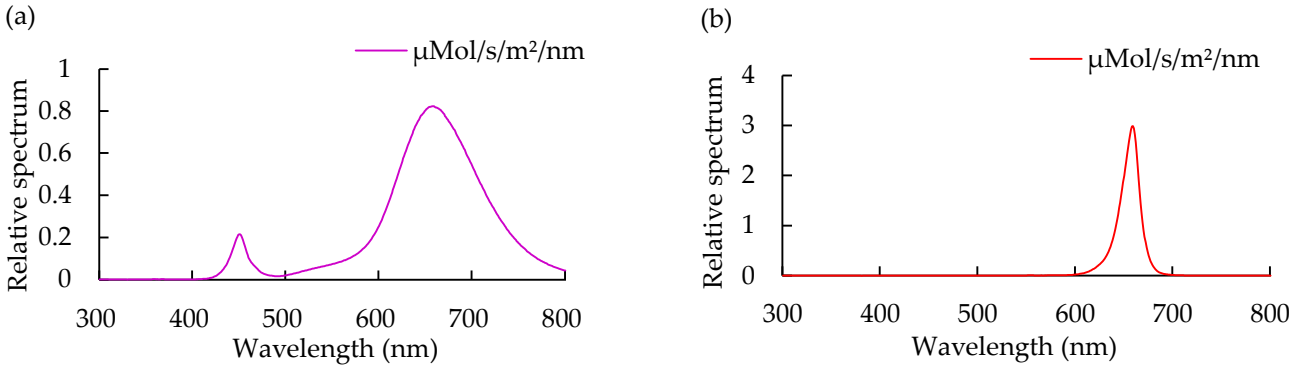


**Figure 9.** Spectral distribution of red/blue lighting (**a**) and red lighting (**b**).

### *4.2. Methods*

The pea variety 'Green Valley Pea No.2' was purchased from Beijing Green Valley Sprouts Co., Ltd., Beijing, China). Pea seeds were soaked in distilled water for 10 h, then placed in Petri dishes with filter paper moistened with 0, 50, and 100 mmol/L NaCl hydroponic solution, with 25 seeds in each Petri dish, and 10 Petri dishes under each concentration gradient, for a total of 750 seeds. The seeds were placed in a shaded environment for germination. The germination percentage of each treatment was counted at 1, 2, and 3 d after sowing.

$$\text{Germination rate (\%)} = \text{number of seeds germinated/total seeds used} \times 100\% \quad (1)$$

To test the salt stress-mitigating effect of red light on pea seedlings, germinated seeds were transplanted in hydroponic cases composed of a plastic box with an internal plastic grid that was illuminated with red/blue lights or red light. Three NaCl solutions at a concentration of 0 (CK), 50, or 100 mmol/L were used for hydroponic cultivation under two light treatments. Each treatment of lighting and salinity combination was replicated three times, with 125 seeds in each of them. Seedlings cultivated in hydroponic cases in the fresh nutrient solution were watered with 0, 50, or 100 mmol/L NaCl solution, respectively, illuminated for 12 h, and kept in the dark for 12 h at 25 ± 1 °C throughout the whole experiment. The hydroponic cases with various light treatments were placed randomly on

the shelves in a density to avoid any possible shading. Lighting tubes were anchored 36 cm above the hydroponic cases. Since the red/blue light at a 4:1 ratio has been regularly used as a supplemental light for leafy vegetables, it was chosen for the three salinity levels as the control groups designated as F0, F1, and F2, while red light in combination with three salinity levels were grouped as R0, R1, and R2.

Morphological parameters such as plant height, plant fresh mass and dry mass, and root characters were measured at 6 and 12 days after seed germination. Five seedlings per treatment were measured with a ruler for their height each time, then separated into their aboveground part and roots, and weighed respectively for their fresh mass using an electronic balance (with an accuracy of ~0.01 g). To obtain their dry mass, both the aboveground part and roots were dried in an oven at 105 °C for 30 min and then kept at 75 °C until they were completely dry. Finally, they were weighed using an electronic balance with an accuracy of 0.0001 g. Fresh root samples were scanned by a root scanner (EPSON EXPRESSION 10000 XL, Epson (Beijing, China) Co., Ltd., Beijing, China), and then analyzed using a root analysis system (WinRHIZO STD4800 LA2400, Regent Co., Ltd., Toronto, ON, Canada), for total root length (cm), total root surface area ($cm^2$), total root volume ($cm^3$), and average diameter of the roots (mm).

Physiological parameters of pea seedlings under each treatment were investigated on the 12th day after sowing. The SPAD value of the 3rd and 4th unfolded leaves at the top of each seedling was measured with a chlorophyll meter to determine the chlorophyll content (TYS-4N Handheld Chlorophyll Analyzer, Beijing Zhongke Weihe Technology Development Co., Ltd., Beijing, China). The content of $K^+$ and $Na^+$ ions was measured with the flame photometric method. The rate of electrolyte leakage used to indicate the permeability and the degree of damage to cell membranes was determined by the protocol described by Dionisio-Sese et al. [57]. Leaves of pea seedlings were sampled, rinsed with tap water, and dried by filter paper. Then, 0.3 g of a sample leaf was cut into small pieces, emerged in deionized water in a 25 mL testing tube, and soaked for 3 h to measure the first EC ($EC_1$) using a conductivity meter (Thunder Magnetic DDS-307A, Shanghai Yidian Scientific Instrument Co., Ltd., Shanghai, China). The second EC ($EC_2$) was determined after the leaf sample in the testing tube was boiled for 30 min and cooled to room temperature. The permeability rate was calculated by EC (%) = $EC_1/EC_2 \times 100\%$. The third unfolded true leaves below the growing tip of all remaining seedlings under each treatment were cut and mixed to determine antioxidant enzymatic activities of superoxide dismutase (SOD), peroxidase (POD), catalase (CAT), and malondialdehyde (MDA). SOD, POD, CAT, and MDA were determined using the SOD (SOD-2-Y), POD (POD-2-Y), CAT (CAT-2-Y), or MDA (MDA-2-Y) detection kit, respectively (Comin Biotechnology Co., Ltd. Suzhou, China) [58]. Briefly, leaf samples maintained under −80 °C were ground with liquid nitrogen. In the $Na_2HPO_4/NaH_2PO_4$ buffer, SOD, POD, CAT, and MDA were extracted by homogenizing on ice (0.1 g leaf tissues for each SOD, POD, CAT, and MDA assay with 1 mL buffer). After the extraction of SOD, POD, CAT, and MDA, the homogenates were centrifuged at $8000\times g$ at 4 °C for 10 min. For the pro assay, the homogenates were shaken in a boiling water bath (90 °C) for 10 min, cooled, and then centrifuged at $1000\times g$ at 25 °C for 10 min.

SOD activity was determined by measuring its ability to inhibit the photochemical reduction of nitroblue tetrazolium (NBT) at 560 nm. One unit of SOD activity (U) was defined as the amount of enzyme that caused a 50% decrease in the SOD-inhibited NBT reduction. The reaction mixture consisted of 240 µL potassium phosphate buffer ($K_2HPO_4/KH_2PO_4$) plus ethylenediaminetetraacetic acid, 510 µL xanthine, 6 µL xanthine oxidase, and 180 µL NBT. Control and blank tubes were performed in the same manner but contained 90 µL supernatant and distilled water, respectively. In the control and blank tubes, the solutions were mixed thoroughly and absorbance levels at 560 nm were determined using a

spectrophotometer (752Pro UV-Vis Spectrophotometer, Lengguang Technology Co., Ltd., Shanghai, China). The results were expressed as units (U) of fresh weight (FW, U/g).

POD activity was determined by measuring the oxidation of guaiacol in the presence of hydrogen peroxide ($H_2O_2$) at 470 nm. One unit of POD activity (U) was defined as the amount of enzyme required to increase the absorbance at 470 nm by 0.01 per min per mL. The reaction mixture consisted of 15 µL supernatant, 270 µL distilled water, 520 µL sodium acetate and acetic acid, 130 µL $H_2O_2$, and 135 µL guaiacol. The reaction mixture was mixed immediately, and the increase in absorbance at 470 nm from 30 s ($A_1$) up to 1.5 min ($A_2$) was determined using a spectrophotometer. POD activity was calculated using the formula POD = 7133 × ($A_2-A_1$)/FW (U/g).

CAT activity was determined by the amount of $H_2O_2$ consumption at 240 nm. One unit of CAT activity (U) was defined as the amount of enzyme catalyzing the decomposition of 1 nmol of $H_2O_2$ per min. The reaction mixture consisted of 100 µL $H_2O_2$ and 20 mL sodium phosphate ($Na_2HPO_4/NaH_2PO_4$) buffer. A 35 µL aliquot of the supernatant was mixed thoroughly with 1 mL reaction mixture, and then the decrease in absorbance at 240 nm ($A_1$) up to 1 min ($A_2$) was determined using a spectrophotometer. CAT activity was calculated using the formula CAT = 678 × ($A_1-A_2$)/FW (U/g).

To measure MDA activity, the reaction mixture consisted of 0.6 mL trichloroacetic acid and thiobarbituric acid. A 0.2 mL aliquot of the supernatant was added and the sample was placed in a boiling water bath (90 °C) for 30 min. After cooling, the mixture was centrifuged at 10,000× *g* at 25 °C for 10 min. The absorbance levels of the supernatant at 532 nm (A532) and 600 nm (A600) were recorded and expressed as U/g FW. The MDA content was calculated using the formula MDA = 25.8 × (A532−A600)/FW (U/g).

### *4.3. Data Analysis*

The experimental data were processed, analyzed, and plotted using EXCEL software. ANOVA and significance tests were performed using SPSS 17.0 data processing software with the LSD method.

## 5. Conclusions

Under salt stress, red light, compared with red/blue (4:1) light, significantly increased the height, aboveground fresh mass, aboveground dry mass, root growth indexes, chlorophyll content, POD enzyme activity, and $K^+/Na^+$ ratio in leaves, but decreased the MDA content, SOD enzyme activity, $Na^+$ content, and stem and leaf electrolyte leakage rate in pea seedlings. In summary, red light can be used to improve the salt tolerance of pea seedlings. The results may provide a theoretical basis for the use of light quality to regulate plant salt tolerance or enhance the tolerance of crop seedlings against abiotic stresses.

**Author Contributions:** The research presented here was carried out in collaboration between all authors. D.F. conceived the idea and designed this study; K.X. carried out the experiment and data analysis; K.X., Y.W., X.S. and H.Z. prepared the first draft of the manuscript; D.F., X.S., C.S. and W.X. revised the manuscript. All authors have read and agreed to the published version of the manuscript.

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**Data Availability Statement:** Data are contained within the article.

**Conflicts of Interest:** The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper. The authors declare no conflict of interest.

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