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Effects of Salt-alkaline Stress on Chlorophyll Fluorescence Characteristics in Leaves of Chieh-qua Seedlings

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Abstract To explore the effect of salt-alkaline stress on the growth and chlorophyll fluorescence characteristics of Chieh-qua seedlings, the Chieh-qua inbred line "C-39" was used as the experimental material, nutrient solution culture was used for the experiment, and different concentrations of alkaline salts $NaHCO_3$ (0, 25, 50, 75, 100, 125 mmol/L) were used for gradient treatment. The results showed that the biomass, plant height and stem thickness of the seedlings showed a decreasing trend with the increase of $NaHCO_3$ concentration, which means that the salt stress seriously inhibited the growth of the seedlings. High concentration of $NaHCO_3$ significantly inhibited the activity of PSII, when the concentration of $NaHCO_3$ reached 75 mmol/L, Fv/Fm and PIabs were significantly lower than CK, while low concentration of $NaHCO_3$ treatment had no significant effect on the activity of PSII. Analysis of JIP-test showed that the relative variable fluorescence VL, VK, VJ and VI at 0.15, 0.3, 2 and 30 ms on the OJIP curve were significantly higher than CK when the concentration of $NaHCO_3$ reached 75 mmol/L, but there were no significant differences between low concentrations. It was explained that high concentration of $NaHCO_3$ treatment inhibited the electron transport of PSII. The increase of VJ was greater than that of VK, indicating that the damage caused by $NaHCO_3$ stress on the donor side was greater than that in the receptor side of the Chieh-qua seedlings. Moreover, the optical energy absorption and distribution in leaves of Chieh-qua seedlings were significantly influenced by high $NaHCO_3$ concentrations treatment. The concentration of reaction centers RC/CSm (Expressed as per unit leaf area) and the proportion of absorbed light energy used for electron transport were decreased. In summary, $NaHCO_3$ treatment inhibited the growth of Chieh-qua seedlings and high-concentration $NaHCO_3$ treatment severely inhibited the Chieh-qua seedlings' photosynthesis. This study provides a theoretical basis for the creation of salt-tolerant Chieh-qua germplasm resources by studying the effects of different concentrations of alkaline salt stress on the growth and photosynthetic performance of seedlings.

Keywords Chieh-qua; Salt-alkaline stress; Chlorophyll fluorescence; PSII

Soil salinization has become one of the main factors restricting sustainable agricultural development in China, and salt-alkali stress is one of the main abiotic stresses that cause crop yield reduction and quality decline (Chen et al., 2014). Chieh-qua *(Benincasa hispida*), also known as hairy gourd, is a one-year-old climbing herbaceous plant belonging to the family Cucurbitaceae and is a variation of wax gourd (Yao and Yang, 2018). Currently, research on Chieh-qua mainly focuses on the breeding of new varieties, identification and evaluation of germplasm resources, and response to high temperature and drought stress etc (Wang et al., 2019a; Wang et al., 2019b; He et al., 2020). However, there are few reports on the study of salt-alkali stress-related to Chieh-qua. It is therefore necessary to carry out research on salt-alkali tolerance in Chieh-qua, which is of great significance to improve its salt tolerance and to improve saline-alkali land.

Photosynthesis is the basis of plant growth and development and is sensitive to abiotic stress. Alkaline salt stress, severely affects plant photosynthesis, which is more harmful to plants than neutral salt stress (Liu et al., 2015). Alkaline salt stress damages the photosynthetic system of plants, and the greater the salt concentration, the more serious the damage. High-concentration stress seriously destroyed the PSII reaction center and reduced the rate of electron transfer (Zhou et al., 2021). Changes in chlorophyll fluorescence directly reflect the status of plant photosynthesis, rapid fluorescence kinetics can determine the extent of damage to plant photosynthetic organs without destroying the plants. Chlorophyll fluorescence determination and JIP-test analysis can systematically analyze photosynthetic parameters and have been widely used in the study of plant response mechanisms to the environment (Song et al., 2011). Zhou et al. (2021) showed that chlorophyll fluorescence kinetic parameters can be used as an important indicator for judging the damage of plants under alkaline salt stress. In this study, Chieh-qua inbred line "C-39" was used to study the effect of different concentrations of $NaHCO_3$ on the growth and chlorophyll fluorescence induction dynamics of Chieh-qua seedlings, in order to explore the physiological mechanism of salt-alkali tolerance in Chieh-qua and provide a theoretical basis for the creation of salt-tolerant Chieh-qua germplasm resources and breeding of new varieties.

1 Results and Analysis

1.1 Effect of $NaHCO_3$ on the growth of seedlings of Chieh-qua

With the increase of $NaHCO_3$ concentration, the dry and fresh weight, plant height and stem diameter of the seedlings decreased (Table 1), and there were significant differences among each treatments. Compared with CK, the shoot fresh weight of T1, T2, T3, T4 and T5 was decreased 15.92%, 45.28%, 53.61%, 62.22% and 71.46%, respectively; Root fresh weight was decreased 23.35%, 26.00%, 53.67%, 68.10% and 71.24%, respectively; Shoot dry weight was decreased 18.38%, 30.14%, 33.33%, 35.05% and 37.62%, respectively; Root dry weight was decreased 8.54%, 19.09%, 23.23%, 39.89% and 61.93%, respectively; Plant height weight was decreased 13.39%, 8.21%, 19.64%, 28.21% and 37.86%, respectively; Stem thickness was decreased 8.29%, 10.46%, 31.50%, 48.03% and 50.47%, respectively. In summary, $NaHCO_3$ treatment significantly inhibited the growth of Chieh-qua.

Table 1 Effect of $NaHCO_3$ on the growth of seedlings of Chieh-qua

Treatment	Shoot fresh weight (g)	Root fresh weight (g)	Shoot dry weight (mg)	Root dry weight (mg)	Plant height (cm)	Stem thickness (mm)
CK	$10.93±0.74^{a}$	$2.59±0.25^{a}$	$1070±69.76^{a}$	$132.67±9.50^{a}$	$14±0.78^{a}$	$5.64±0.70^{a}$
T1	$9.19±1.18^{b}$	$1.99±0.10^{b}$	$873.33±41.63^{b}$	$121.33±3.21^{ab}$	$12.13±1.33^{abc}$	$5.18±0.50^{a}$
T2	$5.98±0.83^{c}$	$1.92±0.07^{b}$	$747.5±28.72^{bc}$	$107.33±10.41^{b}$	$12.85±0.66^{ab}$	$5.05±0.28^{a}$
T3	$5.07±0.58^{cd}$	$1.2±0.09^{c}$	$713.33±90.18^{c}$	$101.67±13.87^{bc}$	$11.25±0.65^{bc}$	$3.87±0.36^{b}$
T4	$4.13±0.36^{de}$	$0.96±0.07^{cd}$	$695±62.45^{c}$	$79.75±6.80^{c}$	$10.05±1.14^{cd}$	$2.93±0.22^{bc}$
T5	$3.12±0.35^{e}$	$0.69±0.07^{d}$	$667.5±56.20^{c}$	$50.5±5.32^{d}$	$8.7±0.88^{d}$	$2.80±0.49^{c}$

1.2 Effects of $NaHCO_3$ treatment on F_v/F_m (A) and PI_{abs} (B) of Chieh-qua seedlings

As the concentration of $NaHCO_3$ increased, F_v/F_m and PI_{abs} of the seedlings showed a decreasing trend, with the change in PI_{abs} being significantly greater than that of Fv/Fm (Figure 1). The F_v/F_m and PI_{abs} values of the T3, T4 and T5 treatments were significantly lower than those of CK, T1 and T2. In addition, there was no significant difference between CK, T1 and T2. Moreover, the F_v/F_m value of T5 was significantly lower than that of T3 and T4. Compared with CK, the F_v/F_m values of T3, T4 and T5 were decreased by 10.51%, 6.12%, and 15.78%, respectively, and the PI_{abs} values of T3, T4 and T5 were decreased by 57.10%, 57.82% and 63.21%, respectively. Therefore, $NaHCO_3$ treatment reduced the overall activity of PSII in Chieh-qua seedlings, and when the concentration reached 75 mmol/L, the PSII activity was significantly reduced.

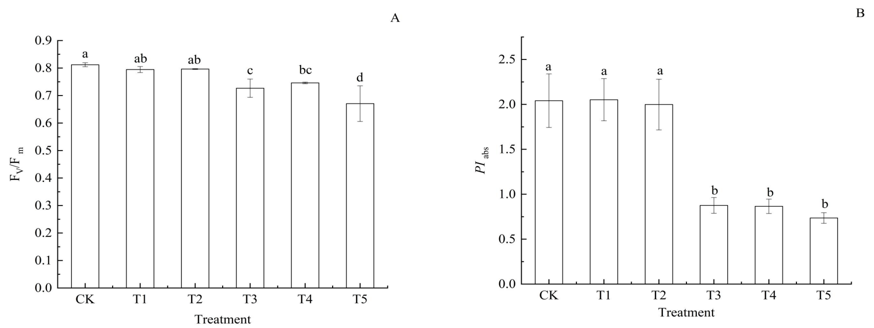

Figure 1 Effects of $NaHCO_3$ treatment on Fv/Fm (A) and PI_{abs} (B) of Chieh-qua

1.3 Effects of $NaHCO_3$ on OJIP curve in the leaves of Chieh-qua seedling.

The effects of $NaHCO_3$ treatment on the chlorophyll fluorescence induction kinetics (OJIP) curve of Chieh-qua seedling leaves were significant (Figure 2A). Due to the high variability of the original OJIP curve under external influences, the curves were standardized and the difference between the standardized curves for each treatment and CK was calculated (Figure 2B; Figure 2C). As the treatment time increased, the relative fluorescence intensity of T3, T4 and T5 was significantly higher than that of CK, T1 and T2 (Figure 2B; Figure 2C). Quantitative analysis of V_J and V_I revealed that the values for T3, T4 and T5 were significantly higher than those for CK, T1 and T2 (Figure 2D; Figure 2E). There was no significant difference between CK, T1 and T2, and the change in V_J was greater than that of V_I. High-concentration $NaHCO_3$ treatment significantly increased the relative fluorescence intensity at I and J points.

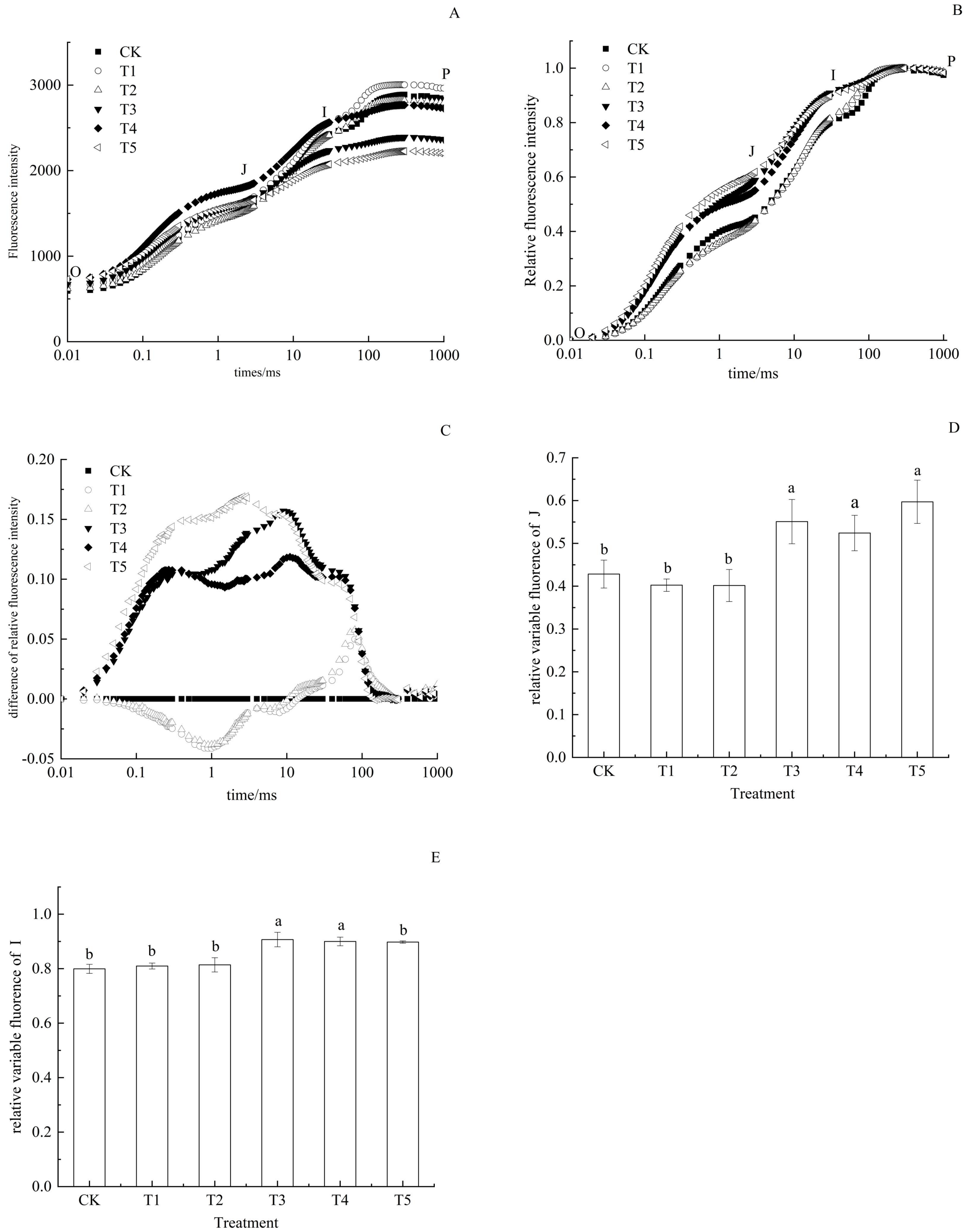

Figure 2 Effects of $NaHCO_3$ on OJIP curve in the leaves of Chieh-qua

1.4 Effects of $NaHCO_3$ on standard O-K and O-J curve in the leaves of Chieh-qua seedling

The relative fluorescence intensity at J point (2.0 ms) and K point (0.3 ms) was defined as 1, and the curves were standardized accordingly (Figure 3A; Figure 3C). It was observed that $NaHCO_3$ treatment significantly affected the standardized O-J and O-K curves. The difference between the two standardized curves for each treatment and CK showed that the fluorescence intensity before K point was significantly higher in T3, T4 and T5 than in CK, T1 and T2 as time elapsed (Figure 3B; Figure 3D). Quantitative analysis of V_K and V_L revealed that the value of V_L for T3, T4 and T5 was significantly higher than that of CK, T1 and T2. Moreover, the value of V_K for T4 and T5 was significantly higher than that of CK, T1 and T2, but there was no significant difference among T3, T4 and T5. The change in V_L was greater than that of V_K. High-concentration $NaHCO_3$ treatment significantly increased the relative fluorescence intensity at L and K points.

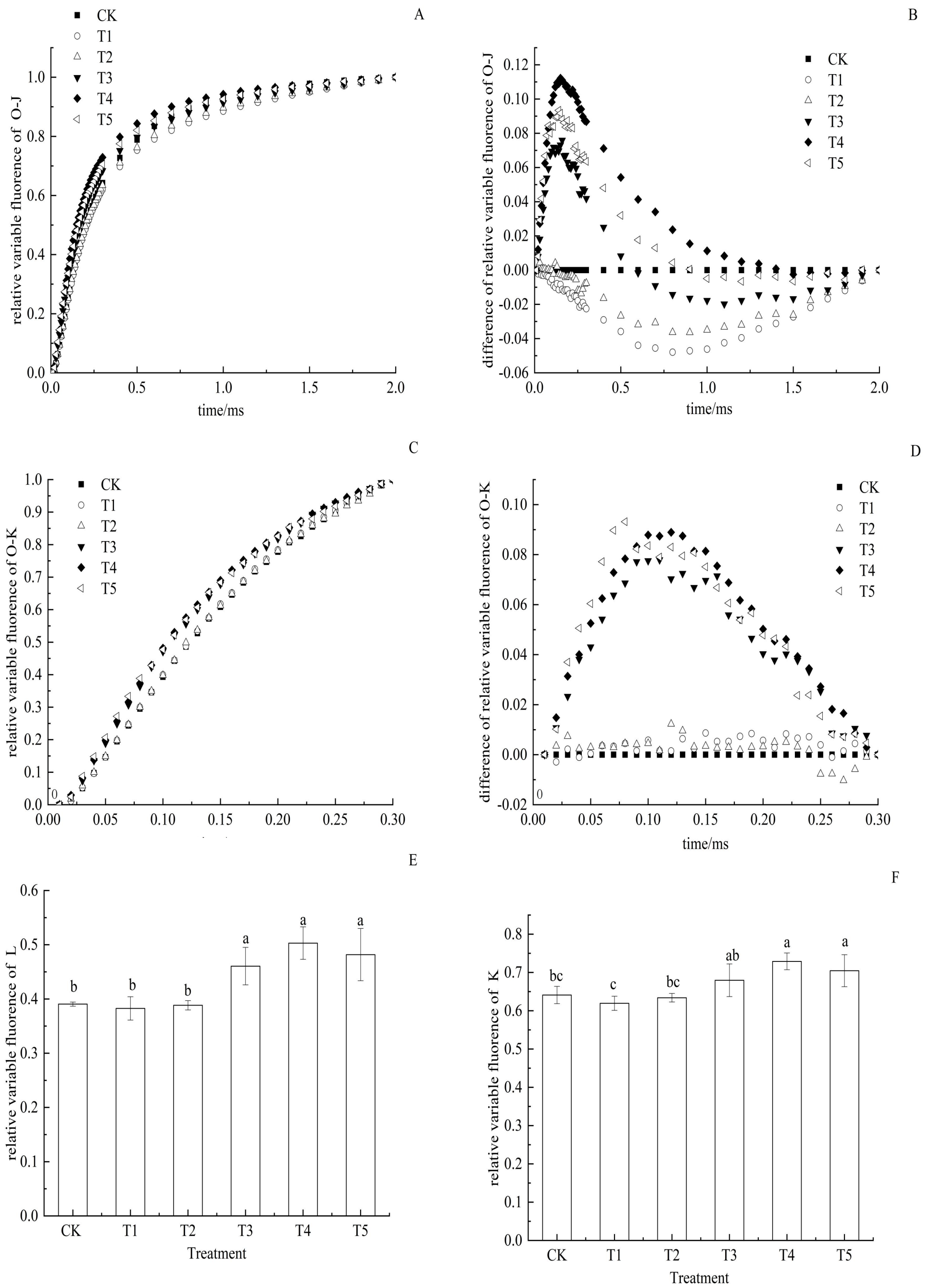

Figure 3 Effects of $NaHCO_3$ on standard O-K and O-J curve in the leaves of Chieh-qua

1.5 Effects of $NaHCO_3$ on energy distribution parameters and RC/CS_m in the leaves of Chieh-qua

The changes in light absorption and distribution parameters of the PSII reaction center in the leaves of Chieh-qua seedlings were significant under T3, T4 and T5 treatments (Figure 4A). As the concentration of $NaHCO_3$ increased, ABS/CS_m, TR_o/CS_m and ET_o/CS_m of the leaves showed a decreasing trend, while DI_o/CS_m showed an increasing trend. ABS/RC and DI_o/RC showed an increasing trend, with a significant increase observed in DI_o/RC, TR_o/RC did not show significant changes, while ET_o/RC showed a decreasing trend (Figure 4A).

As the concentration of $NaHCO_3$ increased, RC/CS_m of Chieh-qua seedling leaves showed a decreasing trend. The values for CK, T1 and T2 were significantly higher than those for T3, T4 and T5, with no significant difference observed among CK, T1 and T2. Compared with CK, T3, T4 and T5 decreased RC/CS_m by 28.67%, 21.17% and 40.13%, respectively (Figure 4B).

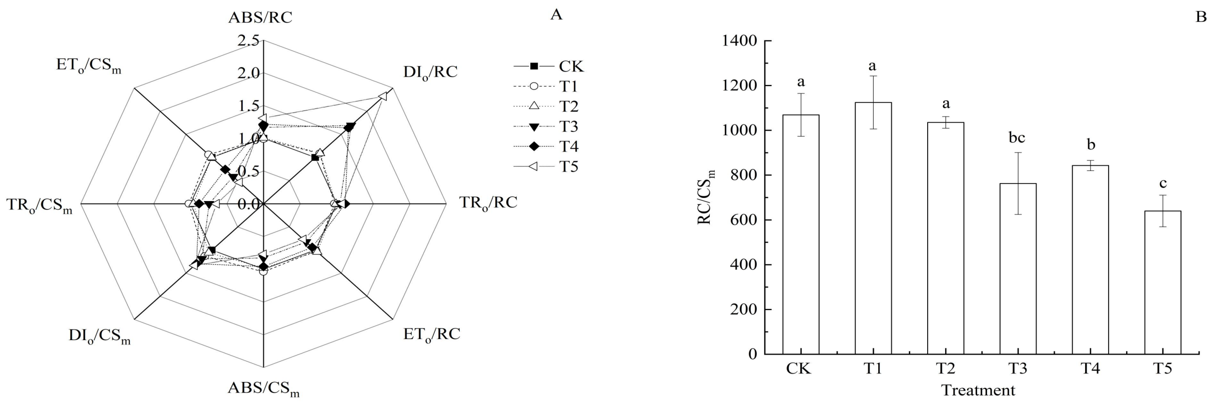

Figure 4 Effects of $NaHCO_3$ on energy distribution parameters and RC/CS_m in the leaves of Chieh-qua

2 Discussion

Changes in biomass reflect the overall response of plants to salt stress, plants respond to salinity stress by slowing growth, redistributing biomass and reducing energy consumption for growth, allowing them to survive under saline conditions (Li et al., 2009). The results of this study showed that with increasing $NaHCO_3$ concentration, the biomass, plant height, and stem thickness of Chieh-qua seedlings decreased, indicating that $NaHCO_3$ severely inhibited their growth, consistent with the findings of Mao et al. (2017).

The fast chlorophyll fluorescence curve (OJIP) contains rich information on PSII photochemical reactions, which can be used to directly analyze the damaged sites of photosynthesis under stress (Zhang et al., 2018). The maximum photochemical efficiency of PSII (F_v/F_m) and the photochemical performance index based on light absorption (PI_{abs}) are important indicators reflecting the efficiency of photoconversion in reaction centers and the degree of inhibition of photosynthetic electron transport (Zhang et al., 2021). The results of this study showed no significant difference in F_v/F_m and PI_{abs} between the low $NaHCO_3$ concentration treatments and CK in the leaves of Chieh-qua seedlings, while at a concentration of 75 mmol/L, both parameters significantly decreased. This indicates that high-concentration $NaHCO_3$ stress significantly reduced the activity of reaction centers and inhibited the rate of photosynthetic electron transport, consistent with the findings of Zhou et al. (2021).

After standardizing the OJIP curve of Chieh-qua seedling leaves according to the O-P, O-J, and O-K parameters, it was found that the L (0.15 ms), K (0.3 ms), J (2 ms), and I points (30 ms) were all significantly higher after high-concentration $NaHCO_3$ treatment compared to control and low-concentration treatment. The presence of the K point indicates inhibition of water-splitting and Pheo (de-magnesiochlorophyll) to Q_A in the electron transfer process, which is a hallmark of damage to the oxygen-evolving complex (OEC) on the PSII donor side (Strasser et al., 2004; Dąbrowski et al., 2016). The results indicate that when $NaHCO_3$ reached 75 mmol/L, a significant increase in the K point was observed (Figure 3D; Figure 3F), indicating that high-concentration $NaHCO_3$ stress severely damaged OEC of PSII on the donor side. The J and I points on the OJIP curve are related to the state of Q_A and plastoquinone (PQ) on the PSII acceptor side, respectively. The relative variable fluorescence of the J point reflects the reduction state of the reaction center or Q_A in PSII (Zhang et al., 2016). High-concentration treatment significantly increased V_J compared to low-concentration treatment and CK, indicating a decrease in electron transfer ability from Q_A to Q_B in the PSII reaction center on the acceptor side. The increase in V_J was significantly greater than V_K, indicating more severe damage on the acceptor side than on the donor side. The I point appears due to the heterogeneity of the PQ pool during electron transfer from Q_A to Q_B (Feng et al., 2002; Li et al., 2005). High-concentration $NaHCO_3$ stress increased the I point, indicating a decrease in electron accepting ability on the PSII acceptor side. This can lead to the accumulation of reactive oxygen species (ROS), which can inhibit the activity of the PSII reaction center and cause photoinhibition (Ding et al., 2014). The rise of the L point is an important sign of thylakoid detachment (Essemine et al., 2012), the behavior of V_L, V_K, V_J, and V_I in Chieh-qua seedling leaves showed a similar trend. When the $NaHCO_3$ concentration reached 75 mmol/L, V_L significantly increased, indicating that high-concentration $NaHCO_3$ stress severely damaged the stability of the thylakoid membrane, leading to a decrease in the coherence of PSII units, disorder of the photosynthetic system, and a reduction in photosynthesis. In summary, high-concentration salt-alkaine stress caused damage to PSII in Chieh-qua seedling leaves, with both the donor and acceptor sides of electron transport inhibited, consistent with the results of Zhang et al. (2022).

When plants encounter environmental stress, they adapt by regulating the allocation of energy, mainly by reducing the absorption of light to prevent photoinhibition (Yin et al., 2019). Under normal growth and development conditions, plants have high light absorption (ABS/CS_m) and capture (TR_o/CS_m) abilities, electron transport rate (ET_o/CS_m), and number of reaction centers (RC/CS_m), and maintaining low thermal dissipation (DI_o/CS_m) (Lu et al., 2022). In this study, increasing $NaHCO_3$ concentration led to a decrease in leaf ABS/CS_m, TR_o/CS_m, ET_o/CS_m, ET_o/RC, and RC/CS_m for Chieh-qua seedlings, with an increase in DI_o/CS_m, ABS/RC and DI_o/RC. Furthermore, the high concentration stress treatment resulted in significantly higher DI_o/RC compared to low concentration stress and CK, while RC/CS_m was significantly lower than low concentration stress and CK. This suggests that salt-alkali stress reduces the ability of leaves per unit area to absorb and capture light energy and the number of active reaction centers while increasing thermal dissipation, which seriously affects the ability of photosynthetic carbon assimilation, consistent with results of Chen et al. (2022). High concentrations of salt-alkali stress cause the deactivation of most PSII reaction centers in Chieh-qua seedling leaves, reducing the antenna pigment's ability to capture light energy.

In conclusion, high concentrations of alkaline salt $NaHCO_3$ stress severely inhibit the PSII electron transport capacity of Chieh-qua seedling leaves. This is mainly manifested by damage to the donor-side oxygen-evolving complex (OEC) and a blockade in the transfer of electrons from Q_A to Q_B on the acceptor side. Additionally, high concentration salt-alkali stress disrupts the balance of light absorption and distribution in Chieh-qua seedling leaves, reducing electron transfer energy while increasing the capacity for thermal dissipation, ultimately leading to inhibited growth of Chieh-qua seedlings.

3 Materials and Methods

3.1 Plant material and growth conditions

The seeds of ‘C-39’, a inbred line, were provided by the Chieh-qua breeding team of Shanghai Academy of Agricultural Sciences. The seedlings were first cultured in 50-well hole trays and cultured in a greenhouse at 25/20 °C (day/night) under light intensity 300 $\mu mol \cdot m^{-2} \cdot s^{-1}$. The photoperiod is 12/12 (day/night). After full development of the second leaf, healthy seedlings of uniform size were selected and transferred into full-strength Hoagland solution and continuously aerated using an air pump. When the third true leaf is fully unfolded, the seedlings are treated as follows: CK: 0 mmol/L、T1: 25 mmol/L、T2: 50 mmol/L、T3: 75 mmol/L、T4: 100 mmol/L、T5: 125 mmol/L. The containers were arranged in a completely randomized block design with three replicates (36 seedlings per treatment), Samples from healthy seedling were harvested after 3 days of treatment. After three days of treatment, growth indexes and chlorophyll fluorescence induction kinetics parameters were measured.

3.2 Determination of growth index and rapid chlorophyll fluorescence kinetic curve

After three days of treatment, six uniform-sized Chieh-qua seedlings from each treatment were selected for growth index measurements. Stem diameter was measured with a caliper, while plant height and root length were measured with a ruler. The fresh weight of the shoots and roots of the plants were determined using a 0.01% electronic scales, and the dry weight of the shoots and roots were determined using a 0.001% electronic scales after drying in an oven.

The Handy-PEA fluorometer (Hansatech, UK) was used to measure the rapid chlorophyll fluorescence induction kinetics curves of the third leaf of each Chieh-qua seedling after dark adaptation for 30 minutes. The OJIP curve points O, L, K, J, I, and P corresponded to fluorescence intensities at 0, 0.15, 0.3, 2, 30, and 1000 ms, respectively. JIP-test analysis was performed on the OJIP curve (Li et al., 2020), and the normalized O-P, O-J, and O-K curves were obtained by subtracting the control (CK) curve, represented as $\Delta V_{O\text{-}P}$, $\Delta V_{O\text{-}J}$, and $\Delta V_{O\text{-}K}$, respectively. The calculation formulas are as follows: $V_{O\text{-}P} = (F_t\text{-}F_o)/(F_P\text{-}F_o)$, $V_{O\text{-}J} = (F_t\text{-}F_o)/(F_J\text{-}F_o)$, and $V_{O\text{-}K} = (F_t\text{-}F_o)/(F_K\text{-}F_o)$, where F_t represents the relative fluorescence intensity at different time points.

The JIP-test analysis of the OJIP curve was also used to obtain other fluorescence parameters, their specific parameters and biological significance are shown in Table 2.

3.3 Data analyzing

Microsoft Excel 2019 was used for statistical processing and SPSS25.0 software was used for significance analysis ($P<0.05$).

Table 2 Parameters used by JIP-test for the analysis of the fluorescence transient OJIP

Fluorescence parameters	Biological significance
Fv/Fm	The maximal PSII photochemical efficiencies
PI abs	performance index on absorption basis
ABS/RC	Absorption flux per RC
TR_o /RC	Trapped energy flux per RC
ET_o /RC	Electron transport flux per RC
DI_o /RC	Dissipated energy flux per RC
ABS /CS_m	Absorption of light energy per CS
TRo /CS_m	Trappingof excitation energy flux
ETo /CS_m	Electron transport flux per CS
DIo /CS_m	Dissipation energy flux perCS
RC/CS_m	Density of RCs per CS

Authors' contributions

LPL and LN is the experimental design of this study and experimental research of executor, LPL complete data analysis and paper writing; ZHM, TSB, DX, WN and WY participated in the experimental design and analysis of experimental results. LN is the proposer and leader of the project, directing experimental design, data analysis, paper writing and modification. All authors read and agree on the final text.

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References

Chen J.B., Zhang F.R., Huang D.F., Zhang L.D., and Zhang Y.D., 2014, Transcriptome analysis of transcription factors in two melon (*Cucumis melo* L.) cultivars under salt stress, Zhiwu Shengli Xuebao (Plant Physiology Journal), 50(2): 150-158.

Chen J.Y., Jiang X., Wu P., Cui H.M., and Cui J.X., 2022, Effects of Ca^{2+} on fast chlorophyll fluorescence and 820 nm reflection kinetics in processing tomato seedlings under salt stress, Zhiwu Yingyang yu Feiliao Xuebao (Journal of Plant Nutrition and Fertilizers), 28(10): 1901-1913.

Dąbrowski P., Baczewska A.H., Pawluśkiewicz B., Paunov M., Alexantrov V., Goltsev V., and Kalaji M.H., 2016, Prompt chlorophyll a fluorescence as a rapid tool for diagnostic changes in PSII structure inhibited by salt stress in Perennial ryegrass, J. Photochem. Photobiol. B., (2016): 22-31. https://doi.org/10.1016/j.jphotobiol.2016.02.001

Ding J.N., Zhang H.H., and Chi D.F., 2014, Response of photosynthesis in leaves of *Sorghum bicolor*×S.sudanense seedlings to phenanthrene polluted soils, Caoye Kexue (Prataculturral Science), 31(9): 1732-1738.

Essemine J., Govindachary S., Ammar S., Bouzid S., and Carpentier R., 2012, Enhanced sensitivity of the photosynthetic apparatus to heat stress in digalactosyl-diacylglycerol deficient *Arabidopsis*, Environmental & Experimental Botany, 80: 16-26. https://doi.org/10.1016/j.envexpbot.2011.12.022

Feng J.C., Hu X.L., and Mao X.J., 2002, Application of chlorophyll fluorescence dynamics to plant physiology in adverse circumstance, Jingjilin Yanjiu (Economic Forest Researches), 20(4): 14-18.

He X.M., Peng Q.W., Liu W.R., Xie D.S., Jiang B., Lin Y.E., Liang Z.J., and Wang M., 2020, A new early-maturing Chieh-qua cultivar'Xinxiu', Yuanyi Xuebao (Acta Horticulturae Sinica) , 47(S2): 2999-3000.

Li F., Xie Y.H., and Qin Y.Y., 2009, Adaptive strategies of wetland plants in salt stress encironment, Shengtaixue Zazhi (Chinese Journal of Ecology), 28(02): 314-321.

Li P.M., Gao H.Y., and Strasser R.J., 2005, Application of the fast chlorophyll fluorescence induction dynamics analysis in photosynthesis study, Zhiwu Shengli yu Fenzi Shengwuxue Xuebao (Journal of Plant Physiology and Molecular Biology), 31(6): 559-566.

Li S.X., Xu T., Li H., Yang W.Y., Lin J.X., and Zhu X.C., 2020, Effects of low temperature on chlorophyll fluorescence kinetics of maize seedlings, Turang yu Zuowu (Soils and Crops), 9(3): 221-230.

Liu J.X., Wang J.C., Wang R.J., and Jia H.Y., 2015, Effects of salt and alkali stresses on photosynthesis in *Avena nuda* seedlings, Ganhan Diqu Nongye Yanjiu (Agricultural Research in the Arid Areas), 33(6): 155-160.

Lu Q.J., Chen L.L., MaY.Y., Liu Y., Zhao Y.W., Zhao B.L., and Sun J.L., 2022, Effects of saline- alkali stress on photosynthetic and chlorophyll fluorescence characteristics of different grape rootstocks, Guoshu Xuebao (Journal of Fruit Science), 39(5): 773-383.

Mao G.L., Liang W.Y., Wang S., Xu X., Zheng R., and Zhu Z.M., 2017, Effects of alkali stress on growth, structure and photosynthetic parameters of *Lycium barbarum* L., Ganhan Diqu Nongye Yanjiu (Agricultural Research in the Arid Areas), 35(4): 236-242.

Song X.L., Hu C.M., Meng J.J., Hou X.L., He Q.W., and Li X.G., 2011, NaCl stress aggravates photoinhibition of photosystem II and photosystem I in *Capsicum annuum* leaves under high irradiance stress, Zhiwu Shengtai Xuebao (Chinese Journal of Plant Ecology), 35(6): 681-686. https://doi.org/10.3724/SP.J.1258.2011.00681

Strasser R.J., Tsimilli-Michael M., and Srivastava A., eds., 2004, Chlorophyll a Fluorescence: A Signature of Photosynthesis, Springer, Dordrecht, pp.321-362. https://doi.org/10.1007/978-1-4020-3218-9_12

Wang M., He X.M., Jiang B., Liu W.R., Lin Y.E., Xie D.S., Liang Z.J., Chen L.H., and Peng Q.W., 2019b, Transcriptome analysis in different chieh-qua cultivars provides new insights into drought-stress response, Plant Biotechnology Reports, 13:663-675. https://doi.org/10.1007/s11816-019-00564-x

Wang M., Jiang B., Liu W.R., Lin Y.E., Liang Z.J., He X.M., and Peng Q.W., 2019a, Transcriptome analyses provide novel insights into heat stress responses in Chieh-qua (*Benincasa hispida* Cogn. var. Chieh-qua How), International Journal of Molecular Sciences, 20(4): 883. https://doi.org/10.3390/ijms20040883

Yao J.X., and Yang F., 2018, Research status and suggestions on Chieh-qua of China, Hubei Nongye Kexue (Hubei Agricultural Sciences), 57(S2): 92-95.

Ying Z.P., Wang Z.Q., Qi M.F., Meng S.D., and Li T.L., 2019, Effects of melatonin application on photosynthetic function in tomato seedlings under salt stress, Shengtaixue Zazhi (Chinese Journal of Ecology), 38(2): 467-475.

Zhang H.H., Feng P., Yang W., Sui X., Li X., Li W., Zhang R.T., Gu S.Y., and Xu N., 2018, Effects of flooding stress on the photosynthetic apparatus of leaves of two *Physocarpus* cultivars, J. For. Res., 29(4): 1049-1059. https://doi.org/10.1007/s11676-017-0496-2

Zhang H.H., Zhong H.X., Wang J.F., Sui X., and Xu N., 2016, Adaptive changes in chlorophyll content and photosynthetic features to low light in Physocarpus amurensis Maxim and Physocarpus opulifolius“ Diabolo”, Peer J, 4: e2125. https://doi.org/10.7717/peerj.2125

Zhang M., Xu G.S., Teng Z.Y., Liu G.J., and Zhang X.L., 2021, Effects of simulated acid rain on growth and photosynthetic physiological characteristics of *Populus simonii* × *P. nigra*, Nanjing Linye Daxue Xuebao (Journal of Nanjing Forestry University (Natural Sciences Edition)), 45(6): 57-64.

Zhang Y.H., Gao D.P., Wang X.L., Shao X.W., Guo L.Y., Huang J.R., and Geng Y.Q., 2022, The Effects of soil salinity on photosystem II of rice seedlings, Guangai Paishui Xuebao (Journal of Irrigation and Drainage), 41: 52-60.

Zhou B.N., Mao L., Hua Z.Z., and Lu J.G., 2021, Effects on photochemical fluorescence properties under salt-alkaline stresses about *Sinocalycanthus chinensis*, Zhejiang Nongye Xuebao (Acta Agriculturae Zhejiangensis), 33(8): 1416-1425.