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Structural and functional stability of photosystem-II in *Moringa oleifera* under salt stress

Sadia Bashir[1,4], Misbah Amir[1*], Faiza Bashir[5], Muhammad Javed[3], Adnan Hussain[4], Saba Fatima[1], Rabia Parveen[1], Aneela Kanwal Shahzadi[1], Shehrooz Afzal[1], Shumaila Raza[1], Tooba Horain[1], Ayesha Iqbal[4], Ayesha Pervaiz[4], Atiq-ur-Rehman[2], Ahsan Ayyaz[1]*, Zafar Ullah Zafar[1], and Habib-ur-Rehman Athar[1]

[1]Institute of Pure and Applied Biology, Bahauddin Zakariya University, Multan 60800, Pakistan
[2]SAKIMS College for boys Bahadurpur, Multan, Pakistan
[3]Department of Botany, University of Education, D.G. Khan Campus, Pakistan
[4]Institute of botany, Quide e Azam campus, University of the Punjab, Lahore 54590, Pakistan
[5]Institute of Plant Biology, Biolgical Research Center, Hungarian Academy of Sciences, Hungary 6726.

***Corresponding authors: misbahamir95@gmail.com, Ahsanayazmsc2015@yahoo.com**

Abstract

The photosynthetic efficiency in plants is affected by salinity. Focus of this study was to observe the consequences of salinity on the rate of photosynthesis in Moringa (*Moringa oleifera* L.) plants. Experiment was conducted under field conditions with 3 replicates and data of treated and non-treated plants was collected accordingly. Photosynthetic rate was affected by different levels of salt stress. The change in photosynthetic was attributes were determined by OJIP and light response curve calculations by using Fluor Pen [FP 100-PS (Photon system, Czech Republic)] and DUAL-PAM-100 (Walz, Germany). Salinity stress decreased chlorophyll a fluorescence characteristic. The significant quantity of electron transport (ϕEo), quantum yield of primary photochemistry (ϕPo), proficiency per trapped excitation (Ψ_o) and performance index of photosystem II (PSII). Performance index (PI_{ABS}) was also declined with salinity in *M. oleifera.* Our results showed that electron transport rate and photosynthetic rate were inhibited by salinity in *M. oleifera.* However, in *M. oleifera* electron transport pathway of PSII was repressed and found varied in plants which are salt resistant. It was concluded that Y(I), ETR(I), Y(II), ETR(II), and Y(NA) were decreased by increasing salinity while NPQ, Y(ND), Y(NO) and Y(NPQ) increased in plants having resistance to salt stress.

Keywords: Salt stress, Light response curve, OJIP, PSII, Non photochemical quenching.

Abbreviations: Area-Area between Fo and Fm, Fo-Fluorescence intensity calculated when all reaction centers of PSII were opened; many other factors may effect this calculated value, Fm-Chlorophyll fluorescence intensity calculated maximum when all the reaction centers of PSII were closed, Mo-Curve slope when fluorescence rise, value of primary photochemistry rate, Vj-Relative variable fluorescence at phase J, Vi-Relative variable fluorescence at 30 ms, Sm- (Area) (Fm – Fo), reflecting the energy required to close the all reaction centers, N-The number which show that by reaching fluorescence to maximum value, how many times QA reduced, ABS/RC-Absorbance per reaction center, DI/RC-Energy dissipation per absorbance, ET/ABS-Electron transport per absorbance, TR/ABS-Trapping energy per absorbance, RC/ABS-Reaction center per absorbance, Fj-Fluorescence intensity at J-phase in induction curve (at 2 ms), Fi-Fluorescence intensity at I-phase in induction curve (at 30 ms), Fv-Fluorescence variable (Fm – Fo), Fv/Fm-Value linked with maximum quantum yield of PSII, Fv/Fo-Value related to the water-splitting complex activity on donor side for stomatal conductance of PSII, PI ABS-the performance index, Y(II)-Quantum yield of PS (II), ETR(II)- Electron Transport rate (II), NPQ Non-photochemical quenching, Y(NPQ)-Quantum yield of non-photochemical quenching by dissipation of energy, Y(NO) Quantum yield of non-photochemical fluorescence quenching by non-dissipation of energy, Y(I) Quantum yield of PS (I), ETR(I) Electron Transport rate (I), Y(ND) Quantum yield of non-photochemical energy emission in reaction centers, incomplete by electrons donor deficiency, Y(NA)-Quantum yield of non-photochemical energy emission in reaction centers, incomplete by deficiency of electron acceptors, qN-Nnon photochemical quenching of inconstant chlorophyll fluorescence, qP-Photochemical quenching of inconstant chlorophyll fluorescence,

Introduction

Moringa oleifera belongs to family *Moringaceae* native species of India and Pakistan (Leone et al. 2015). *Moringa* is a marvel tree and known as "Sohanjna" in local language which has multiple uses such as biogas, water sanitization, and effective for drugs and can be used directly as vegetable. It is usually cultivated almost in every type of soil at height ranging from 600-1800 feet (Jama et al. 1989). The warm tropical areas considered to favorable for its cultivation. It is drought tolerant plant, can withstand acidic and basic soil ranging from pH 5.0-9.0 and to huge range of annual rainfall from 250-3000 mm (Jama et al. 1989).

Plant development and efficiency is greatly influenced by the salinity. It is considered that around 7% property of the world is influenced by salinity and a minimum salinity damage of about 20% plant yield (Munns and Tester et al. 2008). Salinity decreased crop yield by affecting the photosynthetic machinery of crop plants. Salt stress adversely affects the photosynthetic pigments, which consequences in reduced enzymes activity involved in fusion of different photosynthetic pigments with reduced reaction center size and photosynthetic efficiency at PSII (Khalid et al. 2015). In that circumstance's salinity can destroy photosynthetic apparatus, plants have only way to evolve excessive amount of energy in the form of heat (Baker et al. 2008). Salinity stress reduces osmotic potential of soil and may decrease plant water potential, or it may increase ion absorption in plants, in this condition plant can delay its digestion processes (Kalaji et al. 1993).

Salinity stress causes extra storage of ions (sodium and chloride) in plant and reduces plant growth and development (Munns et al. 2008). The assembly of enzymes and large complexes is destroyed by the additional accumulation of these ions. Plants can endorse adverse effects of salinity by collecting compatible solutes like glycine betaine and proline in the chloroplast. The photosystem II (PSII) is protected by these osmoprotectants under salinity stress (Kalaji et al. 2011).

The effects of salinity on photosynthetic rate were determined since long by using gas exchange features, pigments of photosynthesis and chlorophyll a fluorescence kinetic analysis. However, few reports are available on PSII structural stability and functionality under salt stress conditions using Chl a fluorescence analysis. The fundamentals of the OJIP chlorophyll transients has been used when the photosynthetic model is placed at dark, or it is lighted with high pulse of light then fluorescence increases from nominal level of chlorophyll a fluorescence "O" to "J" phases about 2 ms, because of the decrease in QA through photosystem II (PSII), it is showed via fluorescence increase to "I" level about 30ms, because of the satisfying the plastoquinone pool, and lastly, it increases from "I" to "P" level because of the roadblock towards the photosystem I (PSI) electron acceptor side (Kalaji et al. 2011).

JIP-test is non-critical, non-aggressive, useful, fast and reasonable method for the PSII activity analysis (Bussotti et al. 2010). The model of energy drift in thylakoid membranes provides the basis for JIP-test. The association among the activity of photosystem II (PSII), fluorescence indicators and logical terminologies can be determined by JIP-test. This method provides unassuming calculations which show the symmetry among the influx and discharge of energy fluctuation in photosystem II (PSII). JIP test also tells us about the possible destiny of the captivated energy. An evidence of the assembly and role of photosynthetic machinery (generally connected with PSII) can also be observed (Kalaji et al. 2011).

The DUAL PAM-100 is dual pulse amplitude fluorometer through which one can assess PSII and PSI efficiency, linear and cyclic electron transport and development of non-photochemical quenching via xanthophyll cycle. Efficiency of PSI can also be determined by measuring absorbance at 870 and 830 nm light (Schreiber et al. 2008). In addition, it can help in measuring trans-thylakoid proton gradient and membrane potential using optional emitter-detector to calculate the additional important photosynthetic constraints.

Results

Fast chlorophyll fluorescence attributes

The electron transport of photosystem II (PSII) effected by salt stress which could be examined by fast chlorophyll a fluorescence in *Moringa oleifera.* The rise in chlorophyll a fluorescence induction (O-J-I-P) was noticed (Table S1, S2) in control of Moringa plants. High salt concentration has no significant variations in original fluorescence, but fluorescence decreased at J, I and P steps considerably (Table S3, S4). The efficiency of PSII such as performance index; PI_{ABS} was reduced by increasing salt stress from 200 mM to 400 mM in Moringa plants. V_J and V_K were equated below salinity levels (200 mM and 400 mM NaCl) to know the effects of salinity on rate of electron transport at donor side of PSII, at J-phase (2 ms), V_J is comparative variable fluorescence and V_K is comparative variable chlorophyll a fluorescence at 300 µs correspondingly

Salt stress increased V_J and V_K meaningfully. Mo, S_m, N, ϕ_{Po}, Ψo, ϕEo etc were equated below variable salinity levels to determine the salinity effects on rate of electron transport at the acceptor side of PSII. At high salinity levels (200 mM, 400 mM *NaCl*), Mo increased but Sm, N, Ψ_o and ϕ_{Po} were decreased. The salinity effects were observed as that by higher salinity levels (400 mM) ABS/RC increased in *Moringa oleifera* as compared at low salt stress (200 mM) and DIo/RC increased at high salt level (400 mM) while TRo/RC and ETo/RC decreased with increasing salinity (Table S3). Rate of reduction of PSII measured as $M_{o,}$ N, Φ_{Po}. ψ_o is significantly different due to salt stress while $F_{o,}$ Sm, ABS/RC and ETo/RC are significant at level 0.001. Energy flux for energy dissipation per reaction center (DI/RC) and TRo/RC did not change due to salt stress (Table S4, S5).

Light response curve measurements

The valuation of light reaction kinetics is linked with PSI and PSII. As stated (Kramer et al. 2004). A competition found between these parameters as an increase in effectiveness cause decrease in the amount of other two parameters. However, evidence obtained by the alternation in the photochemistry effectiveness and energy discharge by calculating the amount of chlorophyll fluorescence (Ayyaz et al., 2020).

Light Response curve data displayed that Y(I), ETR(I), Y(II), ETR(II), and Y(NA) increased (Figure:2, 5) in control plants and these parameters decreased in plants which were treated with salt (200, 400 mM NaCl). NPQ, Y(ND), Y(NO), Y(NPQ) increased (Table S5, S6) (Figure 3, 5) in both salts stressed (200, 400 mM NaCl) plants and reduced in control plants. While qP, qL and qN increased (Figure 4, 6) in salt treated plants while decreased in control plants. When the effect of salinity on *M. oleifera* was determined at low light intensity 50 µmol m^{-2} s^{-} it showed that the Quantum yield of photosystem II (PSII) 'Y(II)' was 0.256 in control plants, 0.336 in 200 mM salt stressed plants while it was 0.171 in 400 mM salt stressed plants. Electron transport rate 'ETR(II)' was 6.25 in control plants, 7.16 in plants treated with 200 mM NaCl and 3.46 in plants given 400 mM salinity. NPQ was 0.265 in control plants, 0.569 in plants given 200 mM salinity while 0.496 in 400 mM NaCl treated plants. Quantum yield of non-photochemical quenching by dissipation of energy 'Y(NPQ)' was 0.588 in control plants, 0.217 in plants treated with 200 mM salt and 0.39 in plants providing 400 mM salinity.

Quantum yield of non-photochemical fluorescence quenching by non-dissipation of energy 'Y(NO)' was 0.446 in control plants, 0.588 in plants treated with 200 mM salt and 0.801 in plants treated with 400 mM NaCl. The assembly of antenna was also reinforced by the light response curves of chlorophyll a fluorescence parameter. By the photoprotective mechanisms 'qN' inoffensively disperse extra energy as heat. 'qL' is amount of the redox state of the PSII acceptor side (Kramer et al. 2004). At low light intensity 50 µmol m^{-2} s^{-1} Photochemical quenching of variable chlorophyll fluorescence 'qP' in control plants was 0.327, 0.458 in plants giving 200 mM salinity and 0.505 in plants treated with 400 mM NaCl. 'qL' measured in control plants was 0.095, in plants giving 200 mM NaCl it was 0.189 and 0.357 in plants treated with 400 mM salt stress. Non-photochemical quenching of inconstant chlorophyll fluorescence 'qN' was 0.245 in control plants, 0.388 in plants provided 200 mM salinity and 0.37 in plants treated with 400 mM NaCl.

At low intensity of light 50 µmol m^{-2} $s^{-1,}$ quantum yield of PSI 'Y(I)' was 0.47 in control plants, 0.48 in plants treated with 200 mM while it was 0.29 in plants giving 400 mM salt stress. Electron Transport rate (I) 'ETR(I)' was measured as 12.1 in both control plants and the plants given 200 mM NaCl and it was 9.6 in plants treated with 400 mM salinity. Quantum yield of non-photochemical energy emission in reaction centers, incomplete by deficiency of electron acceptors 'Y(NA)' measured as 0.544 in control plants, 0.393 in plants treated with 200 mM NaCl and 0.052 in plants given 400 mM salt stress.

Quantum yield of non-photochemical energy emission in reaction centers, incomplete by electrons donor deficiency 'Y(ND)' was 0.011 in control plants, 0.757 in plants given 200 mM salinity and 0.408 in plants treated with 400 mM salt stress. So, it was noticed that there were little effects on photosynthesis at low salinity level (200 mM NaCl) as compared to high salt stress (400 mM NaCl) (Table 5)

Increase in qP due to salinity and is significant effect at level 0.01. Y(I), Y(II), Y(NPQ), qL, qN are significant at level 0.05. ETR(II), NPQ, Y(NO), Y(NA), Y(ND) are significant at level 0.001 while ETR(I) is non-significant (ns) (Table 6).

Discussion

The quantum yield (F_v/F_m) regulates the PSII efficiency and under adverse ecological state, it predicts the development of plant (Ruban et al. 2015). The results showed that quantum yield decreased as the salinity level increases, whereas in control plants the quantum yield was the maximum. Salinity decreases (F_v/F_m) which cause photoinhibition and it may cause photodamage. Decrease in (F_v/F_m) and increase in F_o are beneficial for the light induced decrease in the photosystem efficiency (Maxwell et al. 2000). Hence, it was proved by this experiment that by increasing salinity, Fo also increased in *Moringa* plants. As decrease in F_v/F_m cause decrease in photosystem II (PSII) quantum yield and it also exaggerated in plants with were provided salt (Maxwell et al. 2000).When the *Moringa* plants were treated with salt then a lot of fluctuations noticed in chlorophyll *a* fluorescence, which include the decrease in $F_v/F_{o,}$ ET_o/RC while V_j, V_I and M_o increased. As similar parameters were used for the results of maximum values and should be understood by attentions as they depend upon each other and they also have correlations. This behavior of decreased F_v/F_o also noticed under water-stressed situations in primeval and progressive plant species and it cause the disturbances in photosynthesis in PSII (Sudhir et al. 2005). During OJIP there was increase from *O* to *P.* By the oxidation of (Q_A) at *O*-phase fluorescence was smallest (Strasser et al. 2004), when Q_A was reduced at *P*-phase it showed the fluorescence yields (Chen et al. 2009). The background of two intermediates such as (J and I) phases are not well categorized (Boisvert et al. 2006), but there were indications that they are connected with the Q_A in reduction state and also related with plastoquinone (Strasser et al. 2004). Researches also showed that there is substantial increase in reaction centers of PSII at J and I phase which designated by V_j and V_i in plants due to ecological strain (Chen et al. 2009), similar comebacks were observed in *Moringa* plants treated with salinity (Jiang et al. 2008).

The primary fluorescence gradient showed the net rate of shutting the reaction centers of PSII (Qiu et al. 2004) and re-oxidized the rate of Q_A which showed the variation in plants by increasing ecological strain (Chen et al. 2009). As *Moringa* plants were treated with different salinity levels, it was observed that the photosystem II (PSII) efficiency and reoxidation rate of Q_A decreased and these variations were best observed at 400 mM NaCl (Chen et al. 2009). Performance index (PI_{ABS}), decreased by the elevation in physical stress (Živčák et al. 2008).

There are three efficient components of Performance index (PI_{ABS}) which are light energy absorption, trapping of energy and energy change into electron transport. It was observed that Performance index absorbance (PI_{ABS}) changed by the two salinity levels. It was also noticed that the performance index absorbance (PI_{ABS}) decreased by the different salinity levels (0 to 400 mM NaCl). In this study it was noticed that there is a great difference in PI_{ABS} in control plants and the plants which were treated with 400 mM NaCl. Our results are matched with the other studies which also indicated the great differences in PI_{ABS} in following salt treated plants (e.g., *Triticum aestivum* and *Acer* spp.). The results showed that the *T. aestivum* are salt stressed (Mehta et al. 2010), the variations in PI_{ABS} were high in salt treated *Moringa* plants in which efficiency of photosystem II (PSII) declined.

The potential quantum yield of PS(II) is demonstrated by Fv/Fm (Lichtenthaler and Babani et al. 2004). AT Fv/Fm , in the donor side of photosystem II (PSII) the thylakoid assembly is harmed (Skórzyńska-Polit and Baszyński et al. 1997). The reduction in Fv/Fm was due to the reduction in Fm that is distinctive to photoinhibition (Ruban et al. 2016). Fm increased by the destruction in the reaction centers of PSII (Krause et al. 1991).

In current study it was cleared that the reduction in Fv/Fm, decrease the rate of electron transport (ETRII) of PSII by salinity. In barley it was observed that the Fv/Fm remained unchanged by salinity but the value of ETRII was decreased (Baker et al. 2008). The sunlight absorbed by the chlorophyll molecules may be used in photosynthesis or discharge as heat energy (Macedo et al. 2008) or it may reemit like light-chlorophyll a fluorescence which is notorious as non-photochemical quenching (Krause and Weis et al. 1991). NPQ and qN these two parameters are related with energy discharge to protect PSII.

The factor of NPQ which decrease the regulation of PSII antenna competence caused by increase [H^+] in lumen, and this increased proton gradient cause the reduction in PSI and

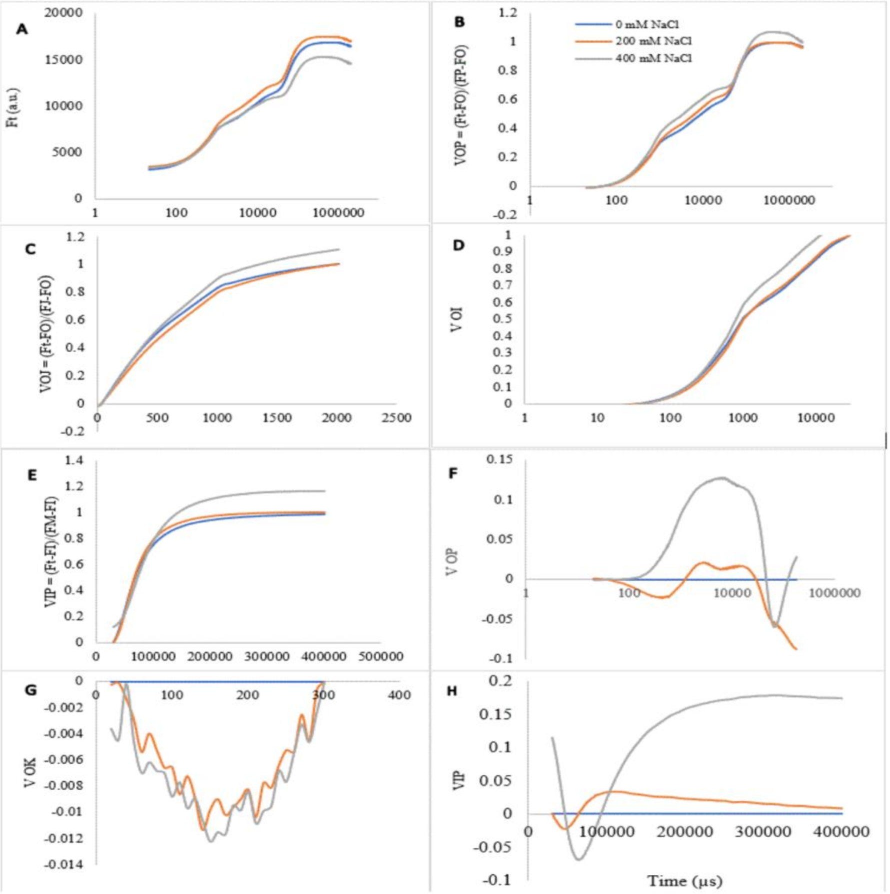

Fig 1. (A) Ft (a.u.), (B) VOP = (Ft-Fo)/(FP-Fo), (C) VOJ = (Ft-Fo)/(FJ-Fo), (D) V_{OI} (E) V_{IP} = (Ft-FI)/(FM-FI), (F) Vop (G) V_{OK} (H) V_{IP} from OJIP the *Moringa oleifera* when four week old plants were subjected to different salinity levels (0, 200 and 400mM.).

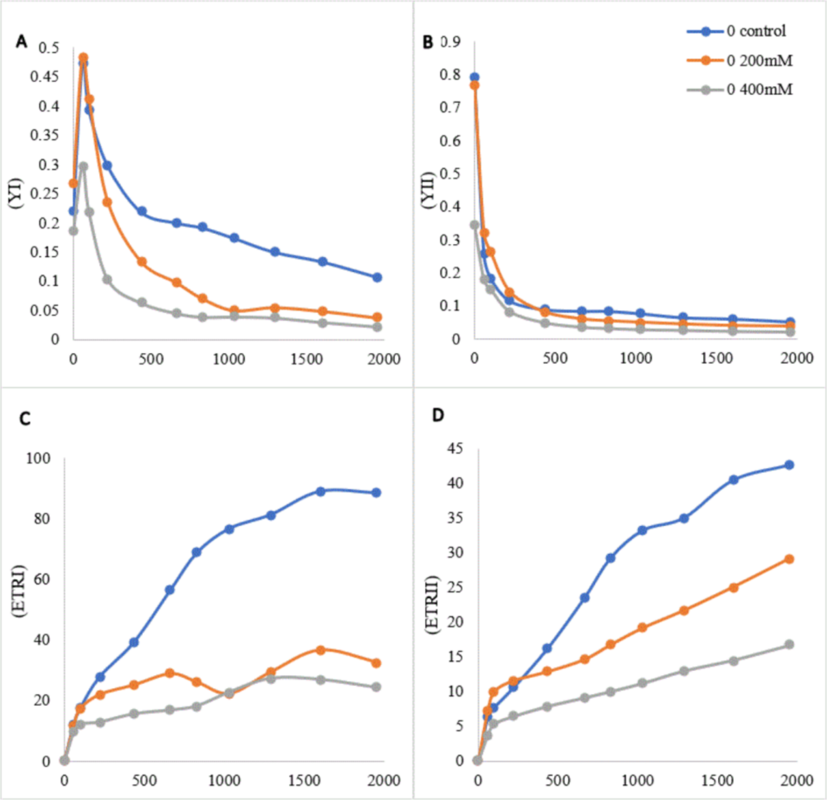

Fig 2. A general legend. (A) Y(I), (B) Y(II), (C) ETR(I), (D) ETR(II) from light curve of *Moringa oleifera* when four-week-old plants were subjected to salt stress (0,200,400 mM) NaCl for three weeks.

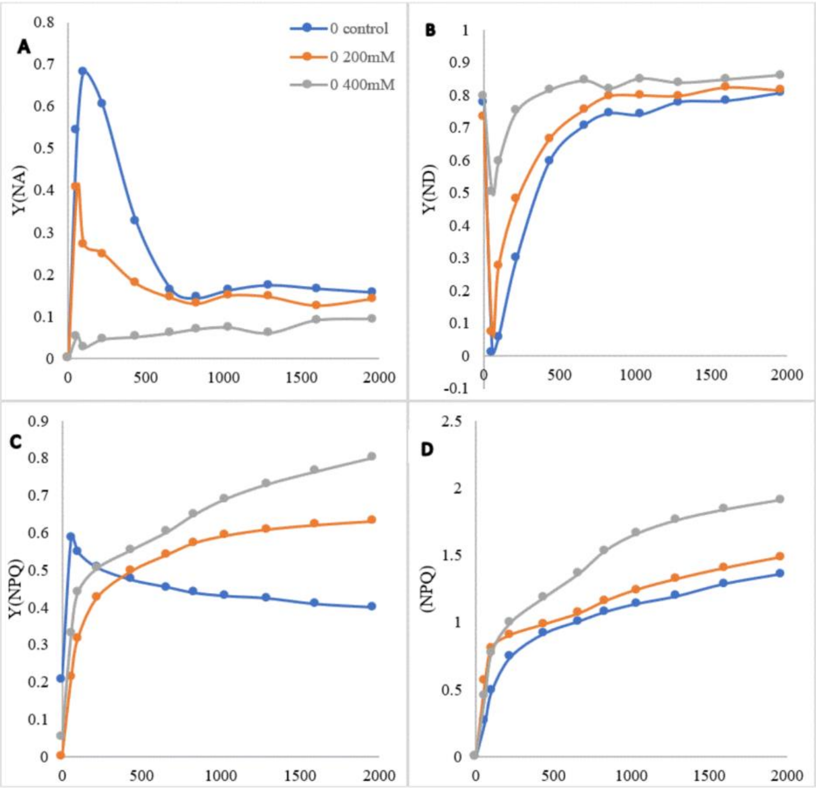

Fig 3. (A) Y(NA), (B) Y(ND), Y(NPQ), (D) NPQ from light curve of *Moringa oleifera* when four-week-old plants were subjected to salt stress (0,200,400 mM) NaCl for three weeks.

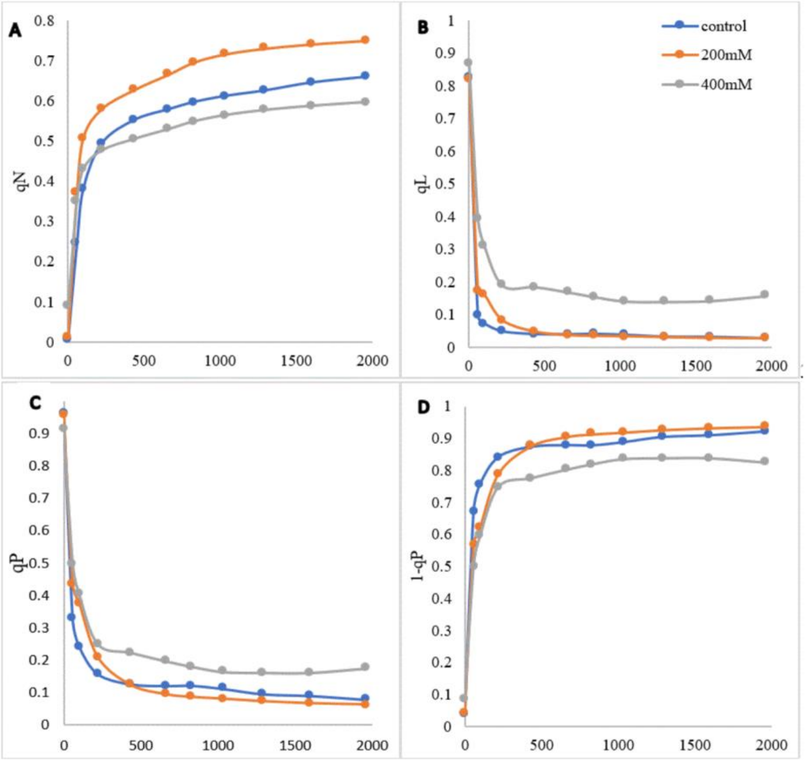

Fig 4. (A) qN, (B) qL, (C) qP, (D) 1-qP from light curve of *Moringa oleifera* when four-week-old plants were subjected to salt stress (0,200,400 mM) NaCl for three weeks.

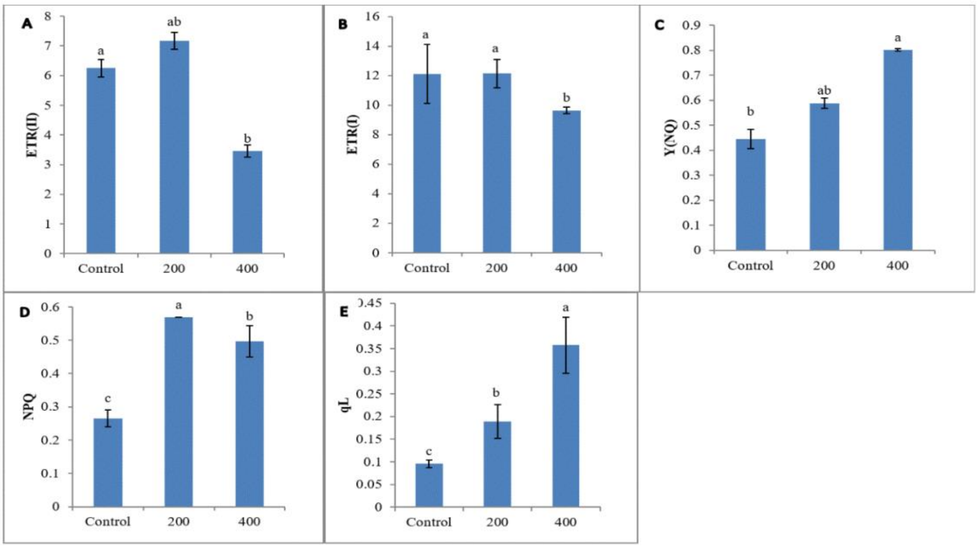

Fig 5. (A) ETR(II), (B) ETR(I), (C) Y(NQ), (D) NPQ, (E) qL from light curve of *Moringa oleifera* when four-week-old plants were subjected to salt stress (0,200,400 mM) NaCl for three weeks.

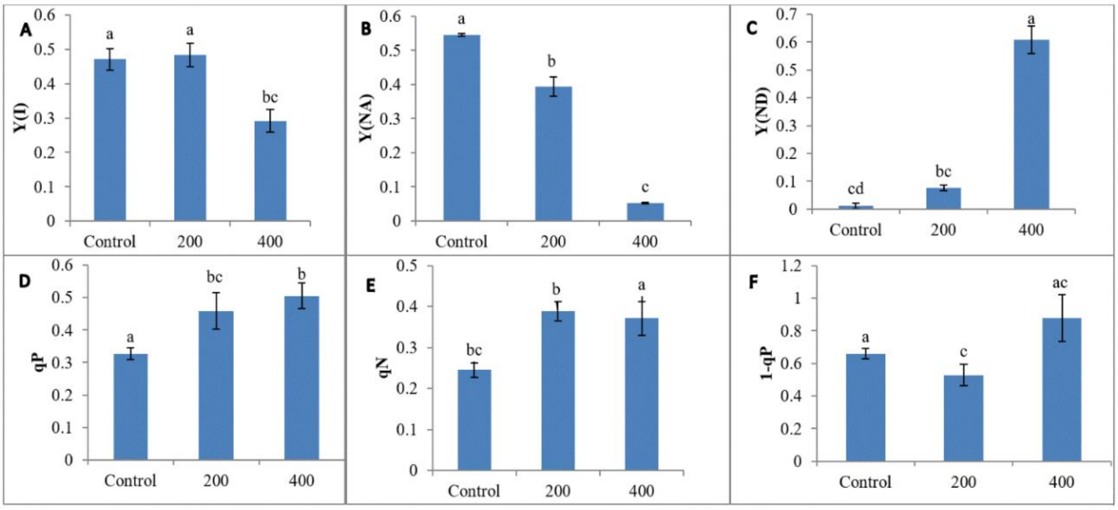

Fig 6. (A) Y(I), (B) Y(NA), (C) Y(ND), (D) qP, (E) qN, (F) 1-qP from light curve of *Moringa oleifera* when four-week-old plants were subjected to salt stress (0, 200, 400 mM NaCl) for three weeks.

PSII oxidoreduction condition (Ruban et al. 2016). Our data showed that the NPQ and qN increased by salt stress in *Moringa*. qL increased in salt treated plants.

The photoinhibition of PSII is related with the open and closed reaction centers of photosystem II (PSII) (Ruban et al. 2015). The current study showed that the qP increased in salt stressed plants. Y(I) is the quantum yield of PSI and is measured by the significant amount of non-photochemical energy discharge (Y(NA) and Y(ND) (Schreiber et al. 2017). Our data revealed that Y(I) and Y(NA) in *Moringa* declined by salinity but Y(ND) is enlarged. It also showed that the lower Y(I) cause the decrease in the electron transport rate (ETRI) of PSI due to salt stress. However, further researches should be done all over the world to know the effects of salinity on *M. oleifera*.

Materials and Methods

Experiment was conducted in Botanical Garden and arranged in completely randomized design comprising 3 replications with three salt levels (i.e. 0, 200, 400 mM NaCl). After washing, seeds were sown in pots, filled with sand. After growth of seedlings for four weeks, salt stress was given in full strength Hoagland nutrient solution. The treatment was repeated after a week. After 21 days of salt stress, OJIP and light curve calculations was done.

Light response curves analysis

Saturation pulse is used to predict light response curve (LC) for calculating the photosynthetic productivity of PSI and PSII. In the presence of actinic light, nominal and extreme chlorophyll fluorescence (Fo and Fm correspondingly) was calculated. Highest productivity of photosystem II (Fv/Fm) was determined by (Fm-Fo)/Fm. PAR (photosynthetically Active Radiation = PAR) was raised from 0, 58, 100, 221, 435, 665, 830, 1033, 1292, 1599, 1957 µmolm^{-2}s^{-1} for 5 minutes at 20 sec pauses by using red actinic light at regular intervals. In the presence of actinic light at 40 sec pauses, saturation pulse (8,000 µmolm^{-2}s^{-} intensity, 800 ms width) was provided for 5 minutes at 20 sec pauses. Next by increasing light, Fs was determined and Fm' and Pm' were measured later for separate saturation pulse. DUAL PAM-100 Software was used to get Rapid light curve and photosynthetically active radiation was provided via constructed in red light discharging diodes (Table 2).

Fast Chlorophyll a Transient (OJIP Test)

Moringa plants were placed in dark and leaves were subjected to continuous light pulse (3500 $\mu molm^{-2}s^{-1}$) where the parameters of chlorophyll a fluorescence were determined. Then data was analyzed in excel (Table 1).

Statistical analysis

Statistical analysis of the data was subjected to a One Way Completely Randomized Analysis of Variance (1WCR ANOVA) by using a COSTAT software (Cohort Software, Berkeley, California).

Conclusion

This study showed the salinity effects on *M. oleifera* could be determined by the OJIP and light response curve. Quantum yield (F_v/F_m and F_v/F_o), photosystem II performance (PI_{ABS}) and electron flux per reaction center (ET_o/RC) decreased with increasing salt stress from 0 mM to 400 mM which reduced the development in parts of the *Moringa* plant. Disturbance of photosynthetic rate in *Moringa* plants treated with salt showed that *Moringa* can withstand low salinity levels (200 mM NaCl) with a small decrease in photosynthesis.

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