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SALT-INDUCED VARIATION IN SOME POTENTIAL PHYSIOCHEMICAL ATTRIBUTES OF TWO GENETICALLY DIVERSE SPRING WHEAT (*TRITICUM AESTIVUM* L.) CULTIVARS: PHOTOSYNTHESIS AND PHOTOSYSTEM II EFFICIENCY

MUHAMMAD ARSLAN ASHRAF[1] AND MUHAMMAD ASHRAF[1]

[1]*Department of Botany, University of Agriculture, Faisalabad, Pakistan*
[*]*Corresponding author's e-mail: ashrafbot@yahoo.com*

Abstract

Variation in salt tolerance potential of two contrasting wheat cultivars (salt tolerant S-24 and moderately salt sensitive MH-97) at different growth stages was observed when these wheat cultivars were exposed to salinity stress in hydroponic culture. Salinity caused a marked reduction in photosynthetic pigments, transpiration and photosynthetic rates, and stomatal conductance at early growth stages in both wheat cultivars, being more prominent in cv. MH-97. In addition, a marked salt-induced alteration was observed in different attributes of chlorophyll fluorescence. On the basis of physiological characterization of these two wheat cultivars at different growth stages, it was inferred that cv. S-24 exhibited higher salinity tolerance at all growth stages in terms of less salinity-induced degradation of photosynthetic pigments, higher photosynthetic rates, maintenance of photosystem II under salinity stress as compared to that in cv. MH-97. In view of the results presented here, it is evident that wheat plants were prone to adverse effects of salinity at early growth stages as compared to later growth stages.

Introduction

Plants grown on saline soils show impaired growth due to salt-induced osmotic effect, nutrient imbalance, specific ionic effect, oxidative damage due to higher levels of reactive oxygen species (ROS) and alterations in endogenous levels of hormones (Ashraf, 2004; Ashraf & Foolad, 2007; Ashraf, 2009; Nawaz *et al*., 2010). Plants growing on salt affected lands often face the problem of physiological drought due to lower water potential of soil caused by the accumulation of soluble salts. Higher levels of toxic ions such as $Na^+$and Cl^- in saline soils result in impairment of *de novo* chlorophyll synthesis and various physiological mechanisms such as gas exchange and chlorophyll fluorescence attributes (Ashraf, 2004; Moradi & Ismail, 2007; Nawaz *et al*., 2010).

Salt stress causes deterioration of a number of potential biomolecules like chlorophyll (Parida & Das, 2005; Shahbaz *et al*., 2011). Salinity-induced decrease in chlorophyll contents is attributed to the decline in endogenous contents of 5-aminolevulinic acid because it acts as a precursor for protochlorophyllide, a precursor of chlorophyll biosynthesis (Santos, 2004). In addition, plants exposed to salt stress exhibit lower levels of glutamic acid which is required for the synthesis of 5-aminolevulinic acid (Beale & Castelfranco, 1974; Santos & Caldeira, 1999; Santos *et al*., 2001; Santos, 2004). Degradation of chlorophyll in salt stressed plants is due to the removal of phytol brought about by the improved activity of chlorophyllase enzyme (Fang *et al*., 1998). The decrease in chlorophyll contents has been studied in a number of plants under saline regimes, e.g., canola (Nazarbeygi *et al*., 2011), maize (Molazem *et al*., 2010), *Arabidopsis* (Huang *et al*., 2005), tomato (Doganlar, 2010), wheat (Khatkar & Kuhad, 2000), sunflower (Santos, 2004), etc. Furthermore, the decline in chlorophyll contents is not the same at distinct ontogenic phases as has been investigated in wheat by Khatkar & Kuhad (2000). Moreover, decreased rate of net CO_2 assimilation to some degree is attributed to reduced chlorophyll contents under salt stress (Ashraf, 2004). Therefore, monitoring the change in chlorophyll contents at different phases of ontogeny is a meaningful approach to pinpoint variation in salt tolerance potential of plants at different developmental stages.

Considerable perturbation in important physiological attributes has been reported in plants exposed to salt stress. For example, salinity stress decreases photosynthetic and transpiration rates, water use efficiency and stomatal conductance in plants (Ashraf, 2004). The decline in net photosynthetic rate is ascribed to closure of stomata in salinity stressed plants (Drew *et al*., 1990; Downton, 1977; Ashraf, 2004). Higher accumulation of soluble salts causes osmotic stress resulting in enhanced production of ABA whose accumulation in leaves reduces rubisco activity, internal CO_2 concentration, stomatal conductance, etc. Photosynthetic tissues are prone to adverse effects of elevated salt concentration in terms of damage to thylakoid membrane. Furthermore, the activity of photosystem II (PSII) is hampered due to reduced chloroplast K^+ contents caused by ionic imbalance under salinity stress (Ashraf, 2004). Higher rates of photosynthesis and active stomatal regulation induce tolerance to plants against salinity stress (Salama *et al*., 1994; Ashraf, 2004). Generally, less salt-induced decline in photosynthesis leads to higher biomass thereby resulting in improved yield (Ashraf, 2004). Salinity-induced decline in photosynthesis has been reported earlier in wheat at the vegetative, boot and reproductive stages (Ashraf & Parveen, 2002; Abdeshahian *et al*., 2010).

Salt-induced decrease in photosynthesis is often linked to the hampered activity of PS II which is more prone to inhibitory effects of salt stress as compared to PS I (Saleem *et al*., 2011). Salt stress degrades some potential proteins (chlorophyll protein, membrane protein) required for active association between thylakoids and phycobilisomes (Garnier *et al*., 1994). Salinity stress disintegrates the thylakoid membranes in the form of

altered protein profile inhibiting the oxygen evolving potential of PS II. Furthermore, this alteration in protein profile limits the transfer of light energy from antenna complex to PS II (Mehta *et al*., 2010). Plants exposed to salt stress improve the conversion efficiency of excitation energy by down regulating the activity of PS II (Lu & Vonshak, 2002). Therefore, measure of damage to PSII using the chlorophyll fluorescence method is an effective approach to understand the inhibitory effects of salinity on photosynthetic apparatus (Saleem *et al*., 2011). The damage to PS II under salt stress has been reported earlier in wheat at the seedling stage (Mehta *et al*., 2010). Likewise, inhibition in the functioning of PS II under saline regimes in rice at the vegetative and reproductive stages has also been studied using the chlorophyll fluorescence technique by Moradi & Ismail (2007).

In view of the above-given contrasting reports, the present study was conducted to determine the adverse effects of salt stress on various physiological attributes of two contrasting wheat cultivars (S-24, salt tolerant and MH-97, moderately salt sensitive) and to draw the relationships between the salt-induced alterations in physiological mechanisms and degree of salt tolerance of these cultivars at different growth stages.

Materials and Methods

A hydroponic experiment was conducted in a wire-house of the Botanical Garden of the University of Agriculture, Faisalabad, to appraise the inherent potential differences in salinity tolerance of two contrasting wheat cultivars (S-24, salt tolerant and MH-97, moderately salt sensitive) at different growth stages. For this purpose, seeds of two wheat cultivars obtained from Department of Botany, University of Agriculture, Faisalabad, were sown on moistened filter papers placed in Petriplates. Nutrient solution with varying concentrations of NaCl (0, 50 100 and 150 m*M*) was used to moisten the filter papers. Eight-day old seedlings were transplanted into styrofoam sheets floating on nutrient solution contained in a plastic tub (45 x 66 x 23 cm). This hydroponic system was aerated for eight hours a day with the help of an electric pump. The weather conditions for entire experimental period were in the range of 27.46-13.75 ºC for average day and night temperature, 77.28-40.71% for average relative humidity and 5.37-0.871 mm for average rainfall. The data for different attributes were recorded at the vegetative, boot and reproductive stages.

Photosynthetic pigments (Chlorophyll *a* and *b*): Photosynthetic pigments were quantified with the help of a procedure described by Arnon (1949).

Gas exchange parameters: Gas exchange attributes were measured as described elsewhere (Ashraf, 2003).

Chlorophyll fluorescence: Chlorophyll fluorescence attributes were recorded with the help of a fluorescence meter (Multimode chlorophyll fluorometer, OPTI-Sciences, OS5P), following the method of Strasser *et al*., (1995).

Experimental design and statistical analysis: The experimental plan was CRD (completely randomized design) with four replications. Data were analyzed using the Costat program (Version 6.303, USA). The means were compared at 5% level of significance (Steel & Torrie 1986).

Results and Discussion

Photosynthetic pigments are important regulators of photosynthesis (Ashraf, 2004; Parida & Das, 2005). However, these pigments are greatly degraded in plants exposed to salt stress (Ashraf, 2004). Likewise, in the present investigation, higher levels of salts in the growth medium resulted in a marked decline in photosynthetic pigments (Chl. *a* & *b*) at different growth stages in both wheat cultivars, being more in cv. MH-97. The salinity-induced degradation of photosynthetic pigments was higher at the vegetative and boot stages in both wheat cultivars as compared to that at the reproductive stage. Such a variable response of plants to stress-induced decline in pigments at different growth stages has been observed earlier in wheat by Khatkar & Kuhad (2000). These scientists stated that enhanced chlorophyllase activity is responsible for the degradation of chlorophyll contents and the activity of this inhibitory enzyme either increased with plant age or remained unaffected. In the present study, chl. *a*/*b* ratio exhibited variable response in both wheat cultivars under salt stress at different growth stages. For example, at the vegetative stage, this ratio exhibited a significant increase at two lower levels of salt (50 and 100 m*M*) in both wheat cultivars. On the other hand, at the boot stage, cv. MH-97 showed an increase in this attribute at 50 m*M* of NaCl, whereas in cv. S-24 a consistent decline in this ratio was evident at the boot stage. In contrast, this ratio remained unaffected at the reproductive stage in cv. MH-97 but salinity stress in growth medium resulted in a consistent decline in this attribute at the reproductive stage in cv. S-24 (Table 1; Fig. 1). This significant perturbation in chl. *a*/*b* ratio at different growth stages could be attributed to the unequal degradation of photosynthetic pigments (Chl. *a* & *b*) under saline regimes (Barber, 1994). The salt-induced degradation of chlorophyll contents is generally more in sensitive as compared to tolerant cultivars as has been observed earlier in pea and wheat (Hernandez *et al*., 1993; Sairam & Srivastava, 2002). These studies are parallel to our results which showed comparatively less decline in photosynthetic pigments in cv. S-24 (salt tolerant) than that in cv. MH-97 (salt sensitive).

Perturbation in different gas exchange attributes due to salt stress is considered as an important indicator of salinity-induced damage to plants (Ashraf, 2004). Likewise, in the present work, a variable response of both wheat cultivars with respect to these attributes was recorded at distinct phases of ontogeny. For example, reduction in photosynthetic (*A*) and transpiration rates (*E*) was minimal at the boot stage in both wheat cultivars as compared to that at other growth stages. Likewise, lower values for stomatal conductance were recorded at the vegetative stage in both wheat cultivars. The other gas exchange attributes such as internal CO_2 concentration, C*i*/C*a* ratio and water use efficiency (*A*/*E*) declined in response to salt stress in both wheat cultivars and the response of these attributes with respect to plant growth stages was markedly variable. Unlike other attributes, intrinsic water use efficiency (A/g_s) of both wheat cultivars increased variably at early growth stages (Table

2; Figs. 2, 3). Such alterations in gas exchange attributes has been reported earlier in wheat at different growth stages by Ashraf & Parveen (2002). For example, these researchers reported a variable decrease in photosynthesis, transpiration rate, stomatal conductance and water use effciency in tolerant and sensitive wheat cultivars at the vegetative and reproductive stages. The decrease in these attributes has also been recorded in canola (Ulfat *et al*., 2007), wheat (Ashraf & Shahbaz, 2003), okra (Saleem *et al*., 2011), sunflower (Hebbara *et al*., 2003), etc. These attributes are interlinked with each other implying that salinity-induced decline in one of these attributes results in alteration in other attributes. For example, decrease in stomatal conductance under salt stress is attributed to higher levels of ABA resulting in stomatal closure (Zheng *et al*., 2001; Parida & Das, 2005; Etehadnia *et al*., 2010). Ultimately, this decreased stomatal conductance results in a concomitant decrease in net photosynthesis, internal CO_2 concentration and transpiration rate (Ashraf, 2004). However, other factors are also held responsible for the decrease in net photosynthetic rate, e.g., inhibited sink activity and enhanced degradation of photosynthetic pigments (Khatkar & Kuhad, 2000; Vasantha *et al*., 2010).

Table 1. Analysis of variance (mean squares) of data for photosynthetic pigments measured at different growth stages of two wheat (*Triticum aestivum* L.) cultivars when grown in salinized hydroponic culture.

S.O.V	df	Chl. a	Chl. b	Chl. a/b
Cultivar (Cv)	1	7.927***	1.4845***	0.805ns
Stage (Stg)	2	1.282***	0.2532***	0.454ns
Salt (S)	3	4.201***	0.5137***	0.564ns
Cv X Stg	2	0.789***	0.1260***	0.517ns
Cv X S	3	0.043 ns	0.0143ns	1.180*
Stg X S	6	0.040 ns	0.0277*	1.261**
Cv X Stg X S	6	0.038 ns	0.0096ns	0.337ns
Error	72	0.098	0.0095	0.370

*, **, ** * = Significant at 0.05, 0.01 and 0.001 levels, respectively
ns = Non-significant

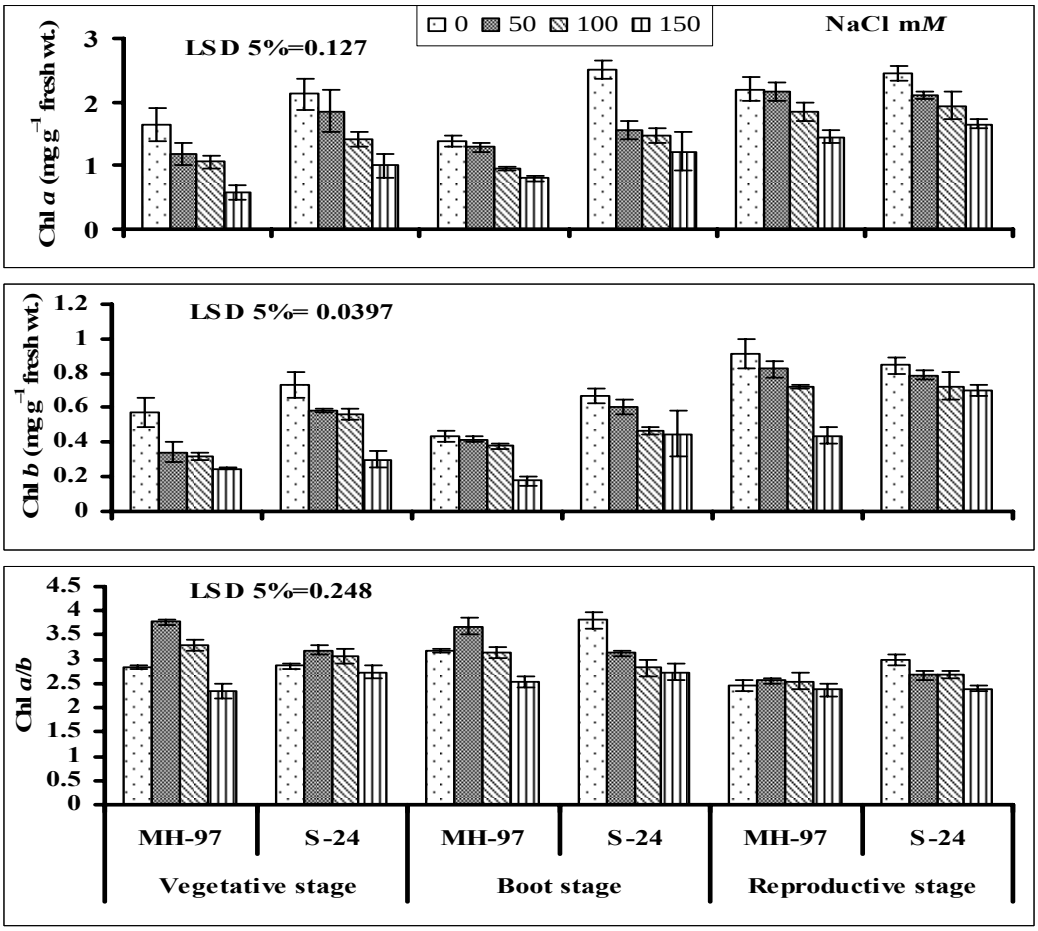

Fig. 1. Photosynthetic pigments of two wheat (*Triticum aestivum* L.) cultivars at different growth stages when grown in a salinized hydroponic culture (*n*=4±S.E.).

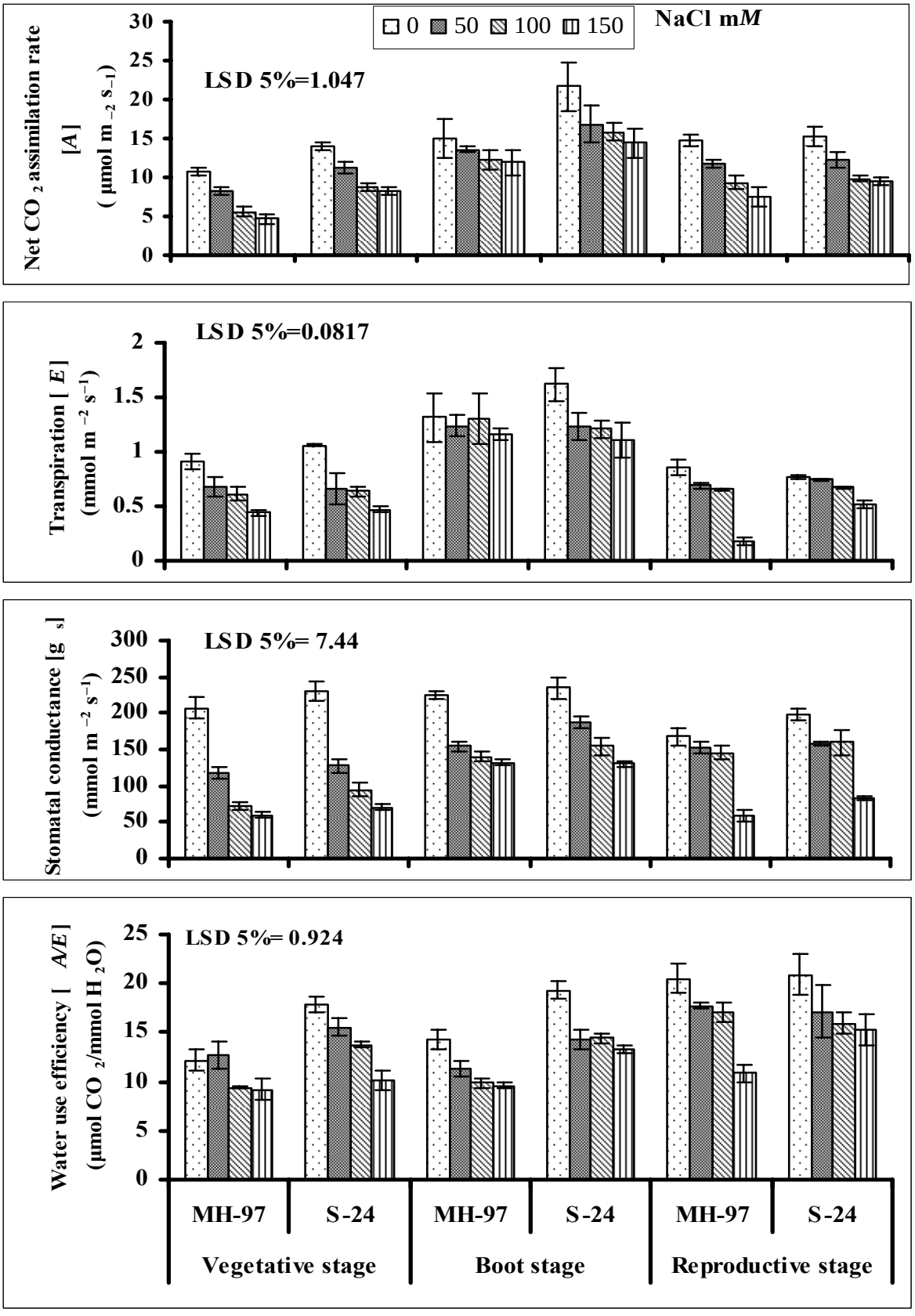

Fig. 2. Gas exchange attributes (*A*, *E*, g_s, *A*/*E*) of two wheat (*Triticum aestivum* L.) cultivars measured at different growth stages in a salinized hydroponic culture (*n*=4±S.E.).

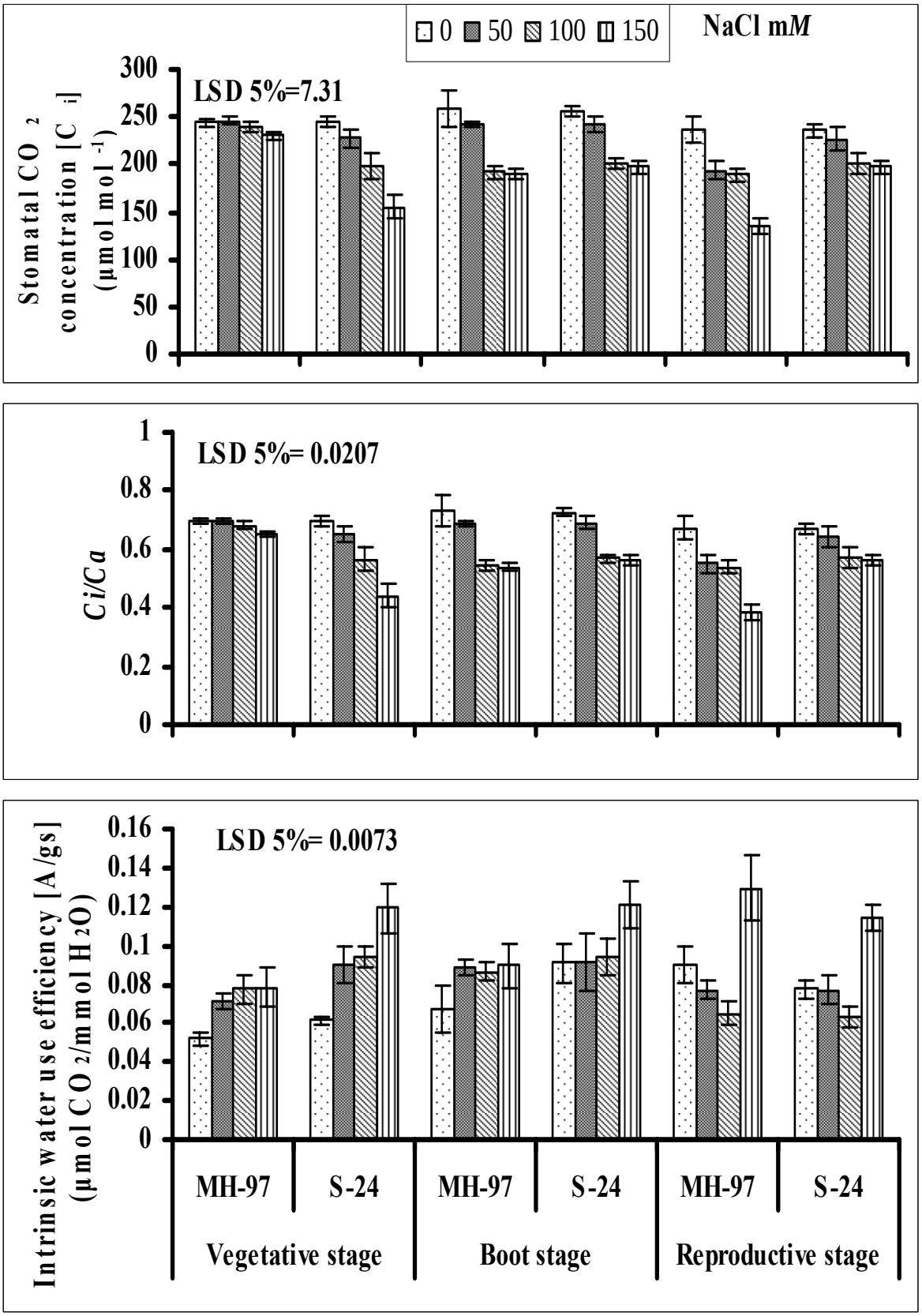

Fig. 3. Gas exchange attributes (*Ci*, *Ci*/*Ca*, *A*/g_s) of two wheat (*Triticum aestivum* L.) cultivars measured at different growth stages in a salinized hydroponic culture (n=4±S.E.).

Table 2. Analysis of variance (mean squares) of data for gas exchange attributes measured at different growth stages of two wheat (*Triticum aestivum* L.) cultivars when grown in salinized hydroponic culture.

S.O.V	df	*A*	*E*	*Ci*	*gs*
Cultivar (Cv)	1	196.76***	0.0098 ns	4189.68***	6501.04***
Stage (Stg)	2	29.74*	1.0762***	9417.39***	5297.13***
Salt (S)	3	159.99***	0.7893***	18134.72***	61861.46***
Cv X Stg	2	298.12***	3.0015***	412.06 ns	13097.14***
Cv X S	3	3.44 ns	0.0149 ns	130.96 ns	6053.12***
Stg X S	6	2.61 ns	0.0786 ns	1555.91***	1091.93**
Cv X Stg X S	6	2.29 ns	0.0277 ns	915.32*	921.09*
Error	72	6.62	0.0403	322.67	334.55
S.O.V	**df**	***Ci/Ca***	***A/E***	***A/g_s***	
Cultivar (Cv)	1	0.0338***	426.470***	0.00220*	
Stage (Stg)	2	0.0760***	43.189***	0.00052ns	
Salt (S)	3	0.1463***	160.190***	0.00580***	
Cv X Stg	2	0.0033 ns	29.059**	0.00240**	
Cv X S	3	0.0011 ns	6.628 ns	0.00220***	
Stg X S	6	0.0126***	11.502*	0.00042ns	
Cv X Stg X S	6	0.0074*	3.162 ns	0.00016ns	
Error	72	0.0026	5.158	0.00032	

*, **, ** * = Significant at 0.05, 0.01 and 0.001 levels, respectively; ns= Non-significant

A = Net CO_2 assimilation rate, *E* = Transpiration, g_s = Stomatal conductance;

A/E = Water use efficiency, A/g_s= Intrinsic water use efficiency

Chlorophyll fluorescence is an excellent measure of functioning of photosystem II (Saleem *et al*., 2011). Likewise, in the present investigation, salinity-induced damage to PS II was detected in both wheat cultivars at all growth stages, being more prominent in cv. MH-97. In the present investigation, different chlorophyll fluorescence attributes were altered markedly by salt stress in both cultivars. For example, in the present study, salinity stress caused a marked decrease in Fo, Qp, leaf Fm, Y and Fv/Fm at different growth stages in both wheat cultivars. However, this salt-induced decrease was more prominent in cv. MH-97 than that in cv. S-24. In contrast, salinity stress caused a significant increase in ETR at the vegetative and boot stages, and NPQ at all growth stages in both wheat cultivars, being more prominent in cv. S-24 (Table 3; Figs. 4, 5, 6). These chlorophyll fluorescence attributes are excellent measures of stress-induced damage to photosystem II. For example, the salt-induced decrease in Fo indicates the loss of energy transfer from antenna complex to reaction centers (Lutts *et al*., 1996; Baker, 2008). Qp tells the proportion of inactivated photosystem II reaction centers (Sayed, 2003; Slapakauskas & Ruzgas, 2005; Moradi & Ismail, 2007; Abdeshahian *et al*., 2010). Likewise, the salt-induced decrease in this attribute could have been due to the separation of light harvesting complex II from the PSII reaction center (Xue-Xia Wu *et al*., 2010). The decrease in Y represents impairment of the ability of plants to repair the salt-induced damage to photosystem II (Allakhverdiev *et al*., 2002; Amirjani, 2010). Similarly, salt-induced decrease in Fv/m corresponds to the salt-induced decrease in maximum fluorescence (Fm) exhibiting the disruption of antenna complex of PSII, increase in dissipation of energy and destruction of photosystem II reaction center (Lutts *et al*., 1996; Maxwell & Jhnson, 2000; Santos *et al*., 2001). Furthermore, the decrease in Fv/m indicates that regeneration of RUBP could have been disrupted by salt stress (Kafi, 2009). In addition, it has been reported that salt-induced increase in photorespiration in C_3 plants like wheat is the main reason for the increase in the rates of electron transport (Megdiche *et al*., 2008). Salinity-induced increase in NPQ exhibits an adaptive energy dissipation process protecting the photosynthetic apparatus against photo-damage (Netondo, *et al*., 2004).

It can be concluded from the results presented here that both wheat cultivars were more sensitive to salinity-induced damage at early growth stages (vegetative and boot) than at later growth stages as is evident from more chlorophyll degradation, marked reduction in various gas exchange attributes and more prominent alterations in a number of chlorophyll fluorescence attributes at the two early growth stages. Furthermore, cv. S-24 was more tolerant to salinity in terms of maintenance of relatively higher photosynthetic rates, less salinity-induced damage to PS-II and photosynthetic pigments as compared to cv. MH-97 at all growth stages.

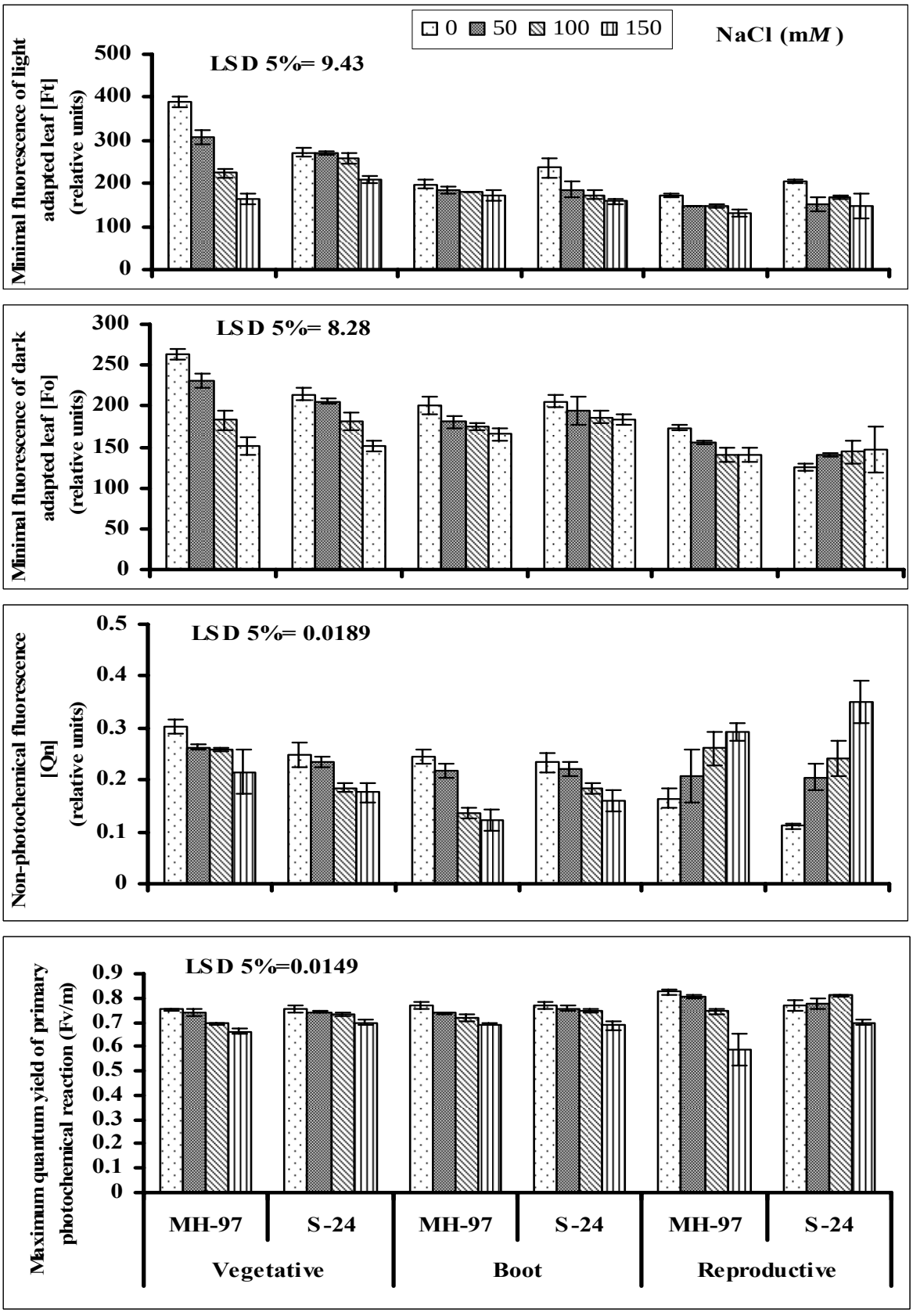

Fig. 4. Chlorophyll fluorescence attributes of two wheat (*Triticum aestivum* L.) cultivars measured at different growth stages in a salinized hydroponic culture (*n*=4±S.E).

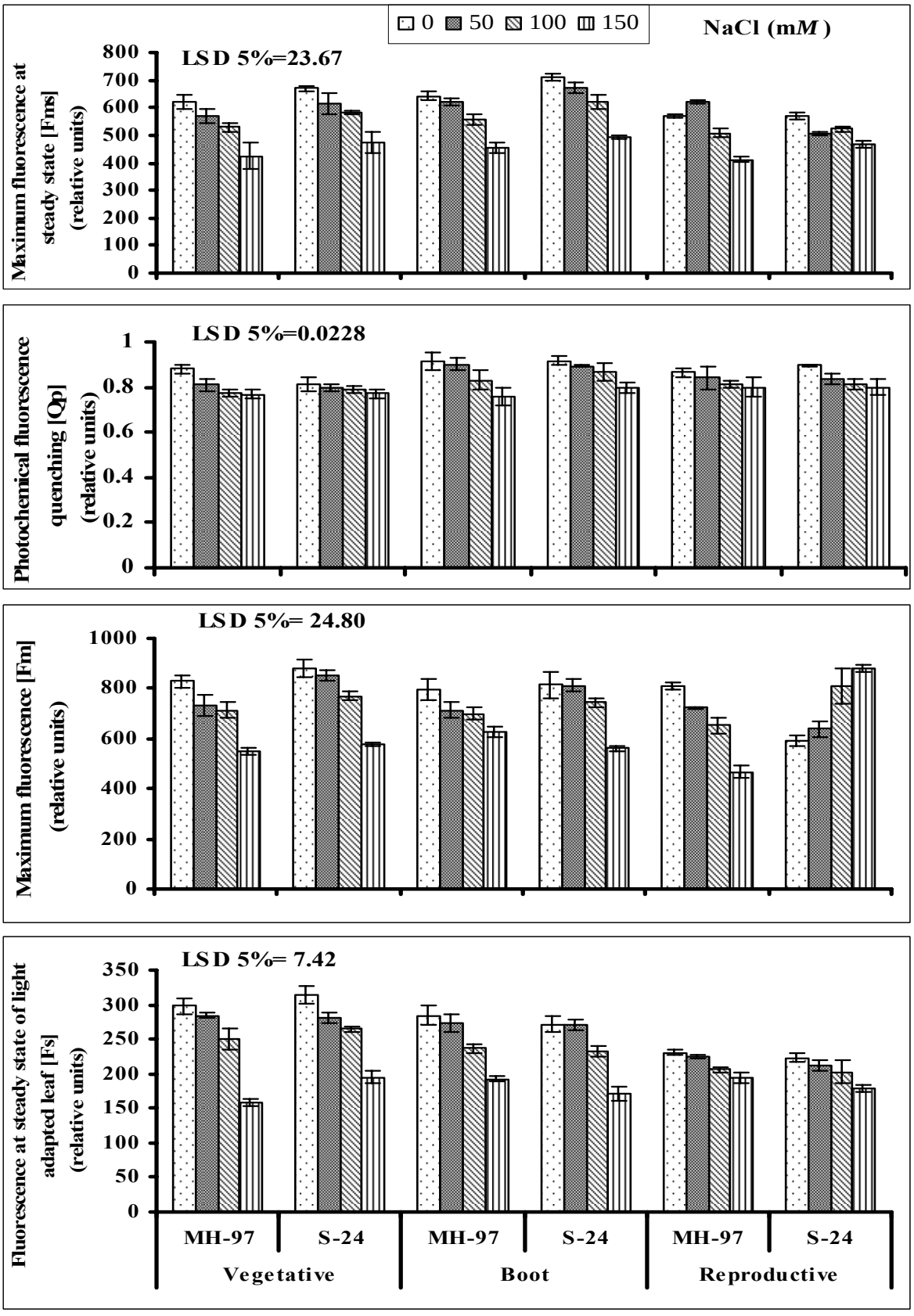

Fig. 5. Chlorophyll fluorescence attributes of two wheat (*Triticum aestivum* L.) cultivars measured at different growth stages in a salinized hydroponic culture (n=4±S.E).

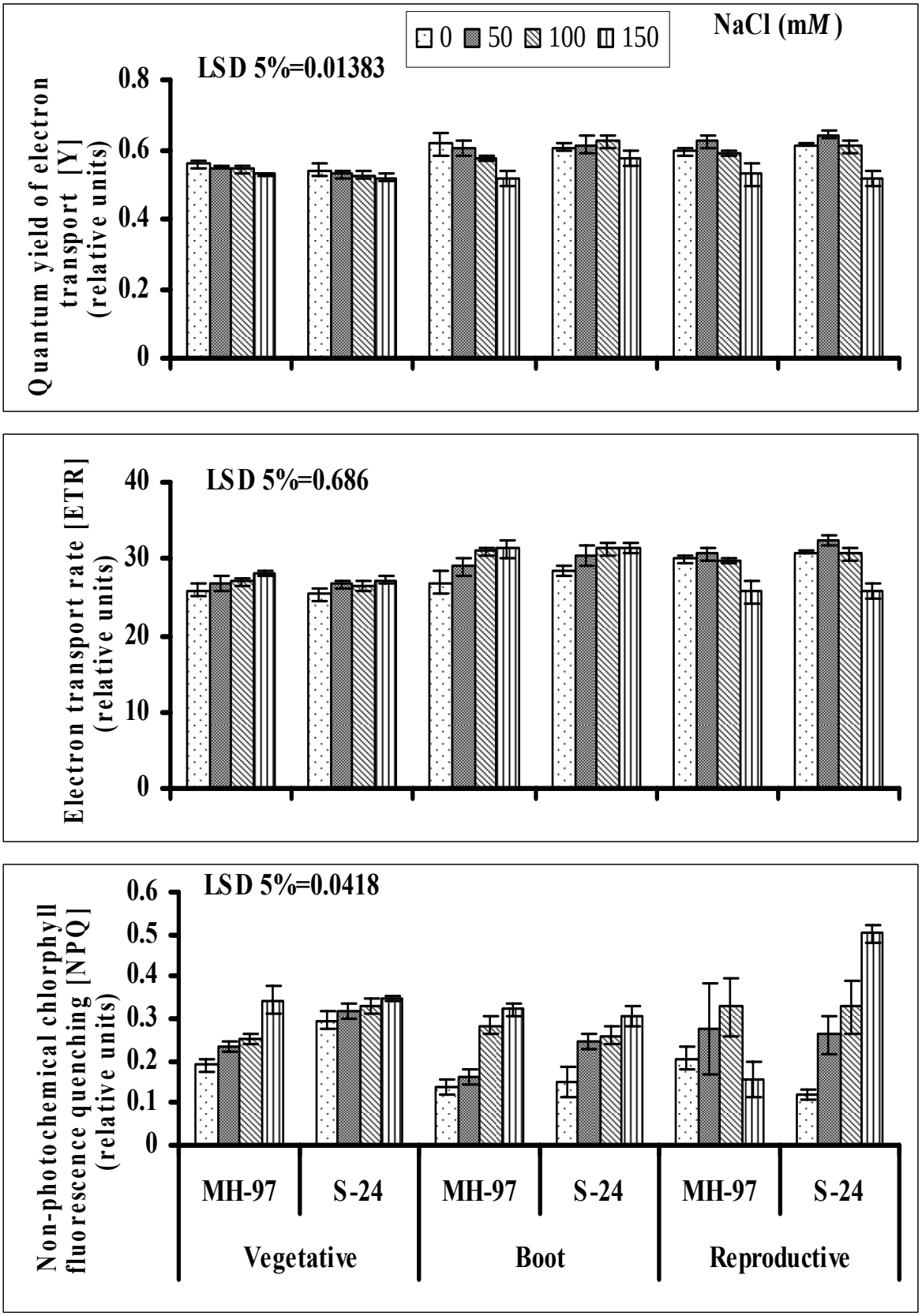

Fig. 6. Chlorophyll fluorescence attributes of two wheat (*Triticum aestivum* L.) cultivars measured at different growth stages in a salinized hydroponic culture (n=4±S.E).

Table 3. Analysis of variance (mean squares) of data for different chlorophyll fluorescence attributes measured at different growth stages of two wheat (*Triticum aestivum* L.) cultivars when grown in salinized hydroponic culture.

S.O.V	df	Ft	Fs	Fo	Fms
Cultivar (Cv)	1	108563.92***	28935.18***	22417.59***	590.04 ns
Stage (Stg)	2	23869.01***	2637.42*	14082.57***	10375.98*
Salt (S)	3	27983.04***	36895.83***	7761.87***	147051.08***
Cv X Stg	2	16763.13***	3318.16*	1551.47*	52475.76***
Cv X S	3	3735.21***	3453.07**	3888.28***	795.68 ns
Stg X S	6	6374.59***	1621.23*	1543.68**	2665.86 ns
Cv X Stg X S	6	3285.80***	260.09 ns	576.66 ns	4763.40 ns
Error	72	600.77	694.82	431.36	2526.50
S.O.V	**df**	**Qp**	**Fm**	**Y**	**Qn**
Cultivar (Cv)	1	0.0188*	8797.51ns	0.0466***	0.0018 ns
Stage (Stg)	2	0.00930*	82.94ns	0.0077**	0.0019 ns
Salt (S)	3	0.04280***	138552.13***	0.0197***	0.0021**
Cv X Stg	2	0.01210*	44715.98***	0.0039*	0.0334***
Cv X S	3	0.00029ns	24485.53***	0.0029*	0.0519***
Stg X S	6	0.00250ns	71173.95***	0.0026*	0.0119**
Cv X Stg X S	6	0.00280ns	30617.77***	0.0005ns	0.0181***
Error	72	0.00270	2727.12	0.0011	0.0032
S.O.V	df	Fv/Fm	ETR	NPQ	
Cultivar (Cv)	1	0.0263***	110.010***	0.0287*	
Stage (Stg)	2	0.0106**	32.887***	0.0491**	
Salt (S)	3	0.0269***	13.425***	0.2217***	
Cv X Stg	2	0.0063*	20.318***	0.1708***	
Cv X S	3	0.0036 ns	31.937***	0.0399**	
Stg X S	6	0.0085***	7.698**	0.1267***	
Cv X Stg X S	6	0.0099***	11.234***	0.0877***	
Error	72	0.0015	2.077	0.0070	

*, **, ** * = Significant at 0.05, 0.01 and 0.001 levels, respectively; ns = Non-significant

Ft = Minimal fluorescence; Fs = Fluorescence at steady state; Fo = Minimal fluorescence; Fms = Maximum fluorescence at steady state; Qp = Photochemical fluorescence quenching; Fm = Maximum fluorescence; Y = Quantum yield of electron transport; Qn = Non-photochemical fluorescence; ETR= Electron transport rate; NPQ = Non-photochemical chlorphyll fluorescence quenching

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