PHOTOSYNTHETICA 41 (2): 273-280, 2003

Assessment of genotypic variation in salt tolerance of early CIMMYT hexaploid wheat germplasm using photosynthetic capacity and water relations as selection criteria

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Abstract

Twenty-five genotypes of early CIMMYT hexaploid wheat were screened for salt tolerance in a glasshouse experiment using photosynthetic capacity and water relation parameters as selection criteria. Under salt stress (150 mM NaCl) the genotypes Frontana, Norin-10, Mayo-54, Noreste-66, and Yaktana-54 excelled all other lines in shoot dry mass, and Na(20)TPP, Penjamo-62, Inia-66, Frontana, Siete Cerros, and Jaral-66 in grain yield per plant in both absolute and relative (percent of control) terms. Although net photosynthetic rate (P_N) declined in all genotypes due to salt stress, it was not helpful in discriminating among genotypes according to salt tolerance. Similarly, no positive relationships of salt tolerance of the genotypes with stomatal conductance, leaf water potential, or turgor pressure were found. Every genotype used its own specific mechanism to tolerate salt stress. However, a large amount of variation in salt tolerance observed in 25 early CIMMYT wheat genotypes can be of considerable practical value for improving salt tolerance in the existing commercial hexaploid wheats.

Additional key words: net photosynthetic rate; stomatal conductance; transpiration rate; *Triticum*.

Introduction

Soil salinisation can reduce plant growth by perturbing biomass allocation, ion relations, water relations, and other physiological processes or by a combination of such factors (Greenway and Munns 1980, Ashraf 1994, Munns 2002). The suppression of growth in many crops is often due to decrease in gas exchange (Seemann and Critchley 1985, Myers *et al.* 1990, Lawlor 1995, Gibberd *et al.* 2002).

Photosynthetic capacity in crop plants is the major component of dry biomass productivity. The final biological or economical yield can be enhanced either by increasing the net photosynthetic rate (P_N), by reducing wasteful respiration, or by optimising assimilate partitioning (Lawlor 1995, Baker 1996, Ashraf and Bashir 2003). In some earlier studies a positive correlation has been found between rate of photosynthesis and final yield. For example, Faver *et al.* (1997) found considerable differences in photosynthetic capacity between modern and obsolete Pima cotton cultivars. They also reported that breeding for yield improved photosynthetic capacity and stomatal conductance (g_s) in advanced cultivars of cotton. The authors thought that further improvement in cotton yield may be achieved through enhanced assimilatory process in modern cultivars. Likewise, the maize cultivars with higher grain yield maintained higher P_N than the low yielding cultivars during plant development (Shuting *et al.* 1997). In asparagus, P_N was positively related to crop yield (Faville *et al.* 1999). Recently, while working with two commercial cultivars (Inqlab-91 and Barani-83) of spring wheat, Ashraf and Bashir (2003) reported that the relatively higher photosynthetic capacity of Inqlab-91 (a high yielding cultivar) at the vegetative stage might have played a significant role in its higher grain yield. In some cultivars of wheat photosynthetic activity is maintained by suppressing sodium uptake (Muranaka *et al.* 2002).

The primary objective of this study was to assess genotypic variation in salt tolerance in a set of early semi-dwarf ‘Green Revolution’ CIMMYT wheat cultivars using photosynthetic capacity and other related attributes as potential selection criteria, and to draw relationships between photosynthetic capacity and growth or grain yield of the lines.

Received 5 May 2003, *accepted* 11 August 2003.

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Materials and methods

Seeds of 25 genotypes of hexaploid wheat were obtained from Dr. T. McNeilly, School of Biological Sciences, University of Liverpool, UK, who originally obtained them from the International Maize and Wheat Improvement Centre (CIMMYT), Mexico. The experiment was conducted in the Botanical Garden of the University of Agriculture, Faisalabad, Pakistan in a netting house supplied with natural sunlight during December–April, 2001–2002. The average day and night temperatures were 29±9 and 15±7 °C, respectively. The average relative air humidity ranged from 41 to 69 % and photoperiod from 10.0 to 12.5 h. The experiment was laid out in a completely randomised design with four replications, 25 wheat genotypes and two salinity treatments.

Twenty seeds of each genotype were sown in each earthen pot (28-cm diameter) containing 8.5 kg of river sand. After 14 d of growth, plants were thinned to six per pot. The plants were grown in full strength Hoagland's nutrient solution for 41 d from sowing, after which NaCl treatment was begun. 2 000 cm^3 of Hoagland's nutrient solution was applied on alternate days to each pot so as the flush through all the salts previously present in the sand. The NaCl treatments used were 0 (without salt) and 150 mol m^{-3} in full strength Hoagland's nutrient solution. The NaCl concentration was increased step-wise in aliquots of 50 mol m^{-3} every day until the appropriate concentration was attained. Each time treatment solutions were applied in the evening.

Two plants from each replicate were harvested at the boot stage. Plants were uprooted carefully and washed with distilled water. After recording fresh mass of both shoots and roots, they were oven-dried at 65 °C for one week and dry mass (DM) was recorded. Remaining four plants were used for attaining seed yield. The data for different gas exchange attributes were recorded also at the boot stage.

Measurements of P_N, transpiration rate (E), g_s, and sub-stomatal CO_2 concentration (C_i) were made on the 3rd leaf from top of each plant using an open system portable infrared gas analyser *LCA-4* (*Analytical Development Company*, Hoddesdon, England). These measurements were made from 10:00 to 12:00 with the following specifications/adjustments: leaf surface area 11.35 cm^2, ambient CO_2 concentration 342.12 µmol mol^{-1}, the mean temperature of leaf chamber was 42.4 °C, ambient pressure (P) 99.95 kPa, molar flow of air per unit leaf area 321.06 mol m^{-2} s^{-1}, PAR at leaf surface was maximum up to 918 µmol m^{-2} s^{-1}.

For the measurements of leaf water relation components the third leaf from top was excised from each plant. Leaf water potential was determined with a Scholander type pressure chamber (*Arimad-2 ELE International*, Tokyo, Japan). For the determination of leaf osmotic potential, the same leaf as used for water potential measurement was frozen in a freezer below –20 °C for 7 d. After this time the frozen leaf material was thawed and all the sap was extracted by pressing the material with the help of a glass rod. The sap was used directly for the determination of osmotic potential in a vapour pressure osmometer (*Wescor 5520*, Logan, USA). The turgor pressure was calculated as the difference between osmotic potential and water potential values. At maturity, grain yields per plant were recorded.

Analysis of variance of data for all attributes was computed using COSTAT computer package (*Cohort Software*, Berkeley, USA). The mean values were compared with the least significance difference test (LSD) following Snedecor and Cochran (1980).

Results

Shoot DMs recorded at the boot stage showed considerable variation in salt tolerance of 25 genotypes of wheat (Tables 1 and 2). Genotypes differed significantly on the basis of shoot DM (p<0.001). Frontana, Norin-10, Mayo-54, Noreste-66, and Yaktana-54 excelled all the lines in mean shoot DM under salt stress. However, Jaral-66, Inia-66, Yaqui-54, and Lerma-52 were the lowest in shoot DM. Frontana, Noreste-66, Yaktana-54, and Kenya-58 had maximum relative shoot DM (more than 70 %), whereas Yaqui-54, Jaral-66, Ciano-67, Lerma Rojo, Lerma-52, and Nainari-60 were lower in % shoot DM having less than 45 % of shoot DM under salinity.

Under salinity, mean grain yield of genotypes Na(20)TPP, Penjamo-62, Inia-66, Frontana, Siete Cerros, and Jaral-66 was higher (grain yield greater than 1.10 g per plant) than that of Norin-10, Nainari-60, and Mayo-54 (less than 0.50 g per plant) (Table 2). On percent of control basis, Norteno-67, Penjamo-62, and Na(20)TPP had higher relative grain yield (more than 40 %) than the other genotypes under salinity (Table 2). In contrast, Norin-10, Mayo-54, Nainari-60, and Pictic-62 had considerably lower (less than 15 %) grain yield than the other genotypes.

Genotypes differed significantly in P_N under salinity (Tables 1 and 3). Higher P_N was observed in Lerma Rojo, Nainari-60, Siete Cerros, and Na(20) TPP, but lower in Mayo-54, Mayo-64, Yaqui-54, and Pictic-62 in terms of both absolute and percent of control values as compared to the other genotypes under salinity.

Salt stress also caused a significant effect on transpiration rate (E) of 25 wheat genotypes (Tables 1 and 3). In both absolute and relative terms, Lerma Rojo,

Table 1. F-values from analyses of variance of data for different growth and gas exchange characteristics, and water relations of semi-dwarf CIMMYT wheats at the boot stage when 41-d-old plants were subjected to 0 (control) or 150 mM NaCl in Hoagland's nutrient solution. **,*** = significant at 0.01 and 0.001 levels; NS = non-significant.

	Source of variation Salt levels (S)	Genotypes (G)	S×G
Shoot dry mass	471.1^{***}	4.96^{***}	2.46^{***}
Grain yield per plant	934.2^{***}	2.41^{***}	2.61^{***}
Net photosynthetic rate	234.4^{***}	5.85^{***}	42.90^{***}
Transpiration rate	225.6^{***}	8.60^{***}	2.68^{***}
Water use efficiency	54.5^{***}	9.89^{***}	1.96^{**}
Stomatal conductance	348.8^{***}	11.09^{***}	5.68^{***}
Sub-stomatal CO_2 conc.	12.2^{***}	4.38^{***}	0.70^{NS}
C_i/C_a ratio	13.1^{***}	4.20^{***}	0.65^{NS}
Water potential	394.0^{***}	16.79^{***}	2.29^{**}
Osmotic potential	356.7^{***}	6.22^{***}	2.81^{***}
Turgor potential	185.6^{***}	22.06^{***}	8.21^{***}

Chris sib, and Na(20)TPP showed comparatively high E under salinity. In contrast, Mayo-64, Yaqui-54, Norin-10, and Noreste-66 showed lower E than the other lines.

Table 2. Shoot dry mass [g] and grain yield per plant [g] of semi-dwarf CIMMYT wheats at the boot stage when 41-d-old plants were subjected to 0 or 150 mM NaCl in Hoagland's nutrient solution. Figures in parentheses are percent of control.

Genotype	Shoot dry mass [g]	Grain yield per plant [g]
Nainari-60	2.89 ± 0.58 (44.7)	0.31 ± 0.07 (8.72)
Yaqui-50	2.26 ± 0.31 (59.3)	0.53 ± 0.20 (25.5)
Frontana	3.90 ± 0.37 (73.6)	1.11 ± 0.29 (25.6)
Noreste 66	3.11 ± 0.23 (73.4)	0.64 ± 0.14 (24.0)
Yaqui-54	1.85 ± 0.24 (31.4)	0.69 ± 0.18 (17.0)
Norteno-67	2.01 ± 0.18 (57.2)	0.93 ± 0.16 (50.4)
Lerma-52	1.87 ± 0.25 (43.4)	0.79 ± 0.30 (25.0)
Tobari-66	2.35 ± 0.56 (61.9)	1.05 ± 0.32 (28.1)
Jaral-66	1.77 ± 0.49 (32.6)	1.10 ± 0.10 (28.9)
Lerma Rojo-64	2.81 ± 0.18 (62.9)	0.64 ± 0.10 (18.1)
Siete Cerros	2.99 ± 0.42 (64.3)	1.11 ± 0.28 (27.3)
Lerma Rojo	2.36 ± 0.32 (44.1)	0.63 ± 0.21 (25.6)
Penjamo-62	3.02 ± 0.17 (60.9)	1.18 ± 0.38 (45.4)
Chris sib	2.81 ± 0.34 (45.7)	1.08 ± 0.22 (28.9)
Pictic-62	3.04 ± 0.69 (51.1)	0.52 ± 0.07 (13.5)
Yaktana-54	3.37 ± 0.53 (71.4)	1.11 ± 0.28 (29.1)
Gabo-55	2.19 ± 0.37 (53.8)	0.52 ± 0.05 (15.8)
Ciano-67	1.94 ± 0.48 (42.7)	1.04 ± 0.25 (30.0)
Sonora-64	2.66 ± 0.19 (53.8)	0.75 ± 0.07 (22.1)
Na(20)TPP	2.21 ± 0.29 (46.0)	1.29 ± 0.19 (40.1)
Inia-66	1.84 ± 0.15 (47.5)	1.13 ± 0.03 (38.7)
Mayo-64	2.70 ± 0.24 (54.5)	0.77 ± 0.03 (16.5)
Mayo-54	3.40 ± 0.15 (59.2)	0.50 ± 0.17 (8.00)
Norin-10	3.49 ± 0.20 (69.6)	0.06 ± 0.01 (2.35)
Kenya-58	2.85 ± 0.37 (70.6)	0.76 ± 0.14 (24.6)

Considerable cultivar difference was observed with respect to water use efficiency (WUE) (Tables 1 and 3). Norin-10 and Nainari-60 were the highest in absolute WUE of all the lines. However, in terms of relative WUE, Nainari-60, Yaqui-50, Norteno-67, Lerma Rojo, Chris sib, Gabo-55, and Na(20)TPP were better (> 90.0 %) than the other genotypes. In contrast, Mayo-54 and Pictic-62 were the worst in WUE.

The response of genotypes to salt stress shown as g_s was different under salinity (Tables 1 and 3). In saline conditions, Nainari-60, Lerma Rojo, and Na(20)TPP were higher in mean g_s (more than 182.4 mmol m^{-2} s^{-1}), although the earlier two genotypes and Gabo-55 and May-54 showed higher relative g_s than the other genotypes. In contrast, Mayo-64, Yaqui-54, and Yaktana-54 were lower (<50 mmol m^{-2} s^{-1}) in this attribute as compared to the other genotypes under salinity. The three genotypes had also low relative g_s.

Sub-stomatal CO_2 concentration (C_i) and relative sub-stomatal CO_2 (sub-stomatal CO_2 concentration/ambient CO_2 concentration; C_i/C_a) varied significantly among the 25 genotypes (Tables 1 and 3). Yaktana-54, Chris sib, and Pictic-62 were the highest, whereas Yaqui-50, Norteno-67, Jaral-66, and Kenya-58 the lowest in mean C_i and C_i/C_a ratio of all the genotypes in saline medium.

Leaf water potential measurements (ψ_w) of 25 wheat genotypes subjected to saline conditions (Tables 1 and 4) showed that Na(20)TPP, Mayo-54, Gabo-55 and Sonora-64 were the lowest, whereas Norin-10 and Chris sib the highest of all the lines in mean ψ_w. Mean leaf osmotic potential (ψ_s) was higher (less negative) in Ciano-67 and Lerma Rojo-64 and lower in Mayo-64, Norin-10, and Nainari-60 as compared to the other genotypes under salinity (Tables 1 and 4). Norin-10, Mayo-64, and Pictic-62 maintained higher, whereas Ciano-67, Gabo-55, and Lerma Rojo-64 lower mean leaf turgor pressure (ψ_p) under salinity as compared to the other wheat genotypes (Table 4). However, ranking of genotypes on the basis of % of control was entirely different to that on the basis of absolute data for different water relation components.

Table 3. Net photosynthetic rate, P_N [μmol(CO_2) m^{-2} s^{-1}], transpiration rate, E [mmol(H_2O) m^{-2} s^{-1}], water use efficiency, P_N/E [μmol(CO_2) mmol^{-1}(H_2O)], stomatal conductance, g_s [mmol m^{-2} s^{-1}], sub-stomatal CO_2 concentration, C_i [μmol mol^{-1}], and sub-stomatal CO_2 concentration/ambient CO_2 concentration (C_i/C_a) of semi-dwarf CIMMYT wheats at the boot stage when 41-d-old plants were subjected to 0 or 150 mM NaCl in Hoagland's nutrient solution. Figures in parentheses are percent of control.

	P_N	E	P_N/E	g_s	C_i	C_i/C_a
Nainari-60	7.13±1.16 (67.9)	2.36±0.28 (69.6)	2.98±0.16 (98.0)	285.00±57.51 (63.0)	261.60±1.87 (98.7)	0.74±0.01 (98.7)
Yaqui-50	4.46±0.89 (62.5)	2.07±0.17 (66.8)	2.13±0.33 (91.8)	100.00±15.66 (52.6)	250.30±10.23 (100.3)	0.71±0.03 (100.0)
Frontana	3.82±0.67 (36.2)	2.15±0.33 (62.7)	1.96±0.47 (63.8)	147.50±10.92 (27.7)	272.70±9.62 (102.4)	0.77±0.02 (101.3)
Noreste-66	2.81±1.49 (28.5)	1.28±0.31 (33.6)	1.88±0.62 (64.2)	65.00±23.24 (24.3)	260.70±19.83 (108.0)	0.74±0.05 (108.8)
Yaqui-54	1.55±0.31 (22.9)	1.06±0.18 (39.0)	1.50±0.28 (53.4)	45.00±5.78 (28.1)	272.80±10.75 (113.3)	0.77±0.03 (113.2)
Norteno-67	4.55±1.53 (51.0)	1.95±0.28 (58.0)	2.33±0.60 (90.7)	102.50±19.65 (41.0)	252.40±10.76 (102.7)	0.71±0.05 (101.4)
Lerma-52	3.15±0.53 (22.5)	1.57±0.37 (48.0)	2.10±0.18 (54.3)	82.50±16.59 (15.8)	260.10±5.78 (107.3)	0.75±0.02 (108.7)
Tobari-66	2.47±0.37 (48.0)	1.44±0.29 (60.5)	1.80±0.27 (82.2)	82.50±2.89 (47.8)	265.50±8.44 (102.4)	0.75±0.02 (102.7)
Jaral-66	3.06±0.47(34.6)	1.78±0.08 (47.6)	1.70±0.21 (63.0)	90.00±19.48 (27.3)	253.80±9.8 (98.4)	0.72±0.03 (98.6)
Lerma Rojo-64	3.30±0.74 (59.8)	1.90±0.25 (67.6)	1.69±0.18 (86.2)	95.00±14.57 (58.5)	268.10±5.89 (100.4)	0.76±0.02 (100.0)
Siete Ceros	6.14±0.95 (53.5)	2.71±0.44 (65.8)	2.27±0.14 (78.5)	157.50±30.69 (32.1)	262.90±3.55 (99.9)	0.77±0.01 (104.0)
Lerma Rojo	7.77±1.29 (80.9)	3.66±0.28 (83.2)	2.12±0.27 (94.6)	222.50±27.69 (62.2)	271.40±12.54 (99.4)	0.77±0.03 (100.0)
Penjamo-62	4.05±0.79 (34.9)	2.67±0.38 (48.3)	1.51±0.21 (64.5)	117.50±26.01 (22.7)	285.30±9.42 (103.0)	0.81±0.02 (102.5)
Chris sib	4.52±0.91 (71.7)	3.55±0.49 (71.7)	1.24±0.10 (96.1)	150.00±26.30 (53.6)	290.00±8.09 (101.5)	0.82±0.02 (101.2)
Pictic-62	1.75±0.20 (21.5)	1.72±0.15 (33.1)	1.02±0.03 (65.0)	65.00±7.46 (20.5)	288.30±1.76 (105.0)	0.82±0.01 (106.5)
Yaktana-54	3.15±1.07 (62.7)	2.40±0.58 (63.8)	1.24±0.14 (89.8)	47.50±11.90 (26.4)	291.50±13.69 (103.9)	0.83±0.04 (103.7)
Gabo-55	5.56±0.64 (97.9)	2.88±0.32 (96.0)	1.94±0.11 (103.4)	152.50±27.28 (85.9)	254.60±3.56 (97.7)	0.74±0.01 (100.0)
Ciano-67	3.47±1.24 (49.6)	1.90±0.33 (67.6)	1.71±0.34 (70.1)	100.00±16.99 (54.8)	268.20±12.25 (106.7)	0.76±0.03 (107.0)
Sonora-64	2.88±0.80 (32.2)	1.42±0.31 (42.1)	2.00±0.15 (76.0)	85.00±12.02 (32.7)	257.10±6.24 (104.2)	0.73±0.02 (104.3)
Na(20)TPP	5.76±1.66 (67.2)	3.19±0.65 (65.9)	1.76±0.14 (97.8)	182.50±54.91 (49.0)	262.70±4.20 (98.5)	0.75±0.01 (100.0)
Inia-66	2.20±0.66 (51.8)	1.65±0.17 (65.2)	1.29±0.26 (77.2)	92.50±15.20 (56.1)	273.80±10.28 (104.7)	0.77±0.03 (104.0)
Mayo-64	1.30±0.28 (12.8)	0.99±0.13 (22.0)	1.34±0.26 (59.3)	37.50±2.89 (12.6)	276.00±11.21 (105.1)	0.78±0.03 (105.4)
Mayo-54	1.03±0.20 (29.7)	1.38±0.45 (68.6)	0.87±0.21 (60.4)	62.50±22.83 (65.8)	285.00±6.35 (107.3)	0.80±0.02 (106.7)
Norin-10	2.96±0.89 (24.1)	1.06±0.27 (47.3)	3.05±0.99 (55.6)	107.00±15.14 (21.1)	259.40±15.89 (102.1)	0.74±0.05 (102.8)
Kenya-58	5.23±0.72 (50.5)	2.36±0.32 (57.7)	2.31±0.43 (87.5)	142.50±11.91 (44.9)	254.40±10.34 (102.2)	0.72±0.03 (101.4)

Discussion

The identification of germplasm of any type within the hexaploid wheat, which has enhanced salinity tolerance is of great potential value (Kingsbury and Epstein 1984, Ashraf 1994, Munns 2002). Such material may be exploited in three ways for direct use in moderately saline soils, provided it includes adaptation to other environmental conditions. It may be used in breeding programs further advancing tolerance and yield potential, to provide material for developing genetically diverse progeny generations within which further cycles of selection may uncover segregants with enhanced salinity tolerance. Salinity tolerance was reported in the early CIMMYT 'Green Revolution' wheat cultivars Tobari-66 and Sonora-64 (Ashraf and McNeilly 1988). In the present study variation in salinity tolerance in a group of semi-dwarf CIMMYT wheats including those related to Tobari-66 and Sonora-64 was examined.

Results of shoot DM and grain yield showed a great variation in salt tolerance in this set of early CIMMYT germplasm. Of the 25 lines, Noreste-66, Frontana, Yaktana-54, and Norin-10 excelled all the lines in shoot DM, whereas Jaral-66, Inia-66, and Yaqui-54 were the lowest of all the genotypes in both mean and relative shoot dry mass. In grain yield, genotypes Na(20)TPP, Penjamo-62, and Inia-66 were the highest (grain yield greater than 1.10 g per plant) and Norin-10, Nainari-60, and Mayo-54 the lowest (less than 0.50 g per plant) of all lines. Thus different lines performed differently in the two growth attributes measured.

Photosynthesis controls growth and dry mass production in plants (Danks *et al.* 1983, Lawlor 1995). However, in the present study non-significant correlation between data (both absolute and percent of control) for P_N and shoot DM or grain yield was observed (Table 5). In addition, there was no consistent relationship between photosynthetic capacity and biomass production of lines of spring wheat differing in degree of salt tolerance. For example, the high biomass producing genotypes Frontana, Yaktana-54, and Noreste-66 had moderate P_N as compared to the other lines. Likewise, the high grain yield producing genotypes, Na(20)TPP, Penjamo-62, and Inia-66 had also moderate values of P_N. These results are in agreement with some earlier studies in which no or little association between growth and P_N is reported in some crop species, *e.g.* in *Hibiscus cannabinus* (Curtis and Läuchli 1986), *Trifolium repens* (Rogers and Noble 1992), spring wheat (Hawkins and Lewis 1993, Ashraf and O'Leary 1996), and Pima cotton (Radin *et al.* 1994).

Table 4. Leaf water potential (ψ_w), osmotic potential (ψ_s), and turgor pressure (ψ_p) of semi-dwarf CIMMYT wheats at the boot stage when 41-d-old plants were subjected to 0 (control) or 150 mM NaCl in Hoagland's nutrient solution. Figures in parentheses are percent of control.

Genotype	ψ_w [–MPa]	ψ_s [–MPa]	ψ_p [MPa]
Nainari-60	1.83±0.12 (69.9)	3.63±0.20 (52.6)	1.80±0.12 (285.7)
Yaqui-50	1.82±0.10 (67.6)	2.86±0.14 (74.5)	1.04±0.07 (114.3)
Frontana	1.74±0.15 (77.0)	2.35±0.07 (70.2)	0.61±0.09 (196.8)
Noreste-66	1.73±0.11 (77.0)	2.56±0.21 (63.7)	0.83±0.16 (122.0)
Yaqui-54	1.70±0.10 (72.9)	2.85±0.35 (52.3)	1.15±0.25 (201.7)
Norteno-67	1.66±0.03 (81.3)	2.75±0.18 (71.3)	1.09±0.16 (187.9)
Lerma-52	1.81±0.07 (76.2)	2.72±0.16 (68.7)	0.90±0.05 (147.5)
Tobari-66	1.84±0.09 (68.5)	2.72±0.20 (51.8)	0.88±0.11 (440.0)
Jaral-66	1.61±0.17 (74.5)	2.44±0.05 (77.0)	0.84±0.15 (100.0)
Lerma Rojo-64	1.69±0.07 (78.1)	2.17±0.12 (74.2)	0.48±0.06 (87.3)
Siete Cerros	1.47±0.13 (68.0)	2.35±0.28 (71.9)	0.88±0.14 (127.5)
Lerma Rojo	1.45±0.10 (73.1)	3.15±0.18 (49.2)	1.70±0.11 (346.9)
Penjamo-62	1.26±0.02 (89.7)	2.81±0.30 (64.8)	1.55±0.28 (224.6)
Chris sib	1.13±0.07 (77.0)	2.76±0.16 (59.8)	1.63±0.12 (168.0)
Pictic-62	1.36±0.03 (83.1)	3.34±0.21 (67.1)	1.98±0.18 (180.0)
Yaktana-54	1.73±0.14 (65.9)	3.47±0.55 (44.4)	1.74±0.43 (457.9)
Gabo-55	1.98±0.16 (58.1)	2.38±0.09 (62.2)	0.40±0.10 (70.2)
Ciano-67	1.70±0.05 (85.9)	2.15±0.24 (69.8)	0.29±0.04 (120.8)
Sonora-64	1.94±0.14 (64.4)	3.04±0.12 (85.8)	1.10±0.06 (80.8)
Na(20)TPP	2.02±0.08 (73.3)	2.83±0.10 (83.7)	0.82±0.08 (92.1)
Inia-66	1.74±0.04 (81.6)	2.41±0.12 (83.0)	0.67±0.09 (115.5)
Mayo-64	1.76±0.10 (72.7)	3.84±0.21 (54.4)	2.08±0.11 (214.4)
Mayo-54	2.00±0.01 (69.0)	3.42±0.40 (58.2)	1.42±0.40 (232.8)
Norin-10	0.83±0.04 (77.1)	3.70±0.29 (57.6)	2.87±0.25 (192.6)
Kenya-58	1.80±0.06 (73.3)	2.64±0.10 (65.1)	0.84±0.05 (120.0)

In wheat cultivars the relationship of P_N and grain yield may be improved by high ear photosynthetic activity (Wang *et al.* 2001).

The effects of salt stress on photosynthesis have been a subject of controversy for many years, and conflicting results have been reported depending on the plant material and the experimental procedures. For example, Lawlor (1995) advocated that although photosynthesis is the main phenomenon for biomass production, a correlation between photosynthetic capacity and grain yield is rarely found. However, the lack of correlation between P_N and grain yield does not mean that photosynthesis is not important for grain yield. The absence of a correlation between these two attributes could be partly due to the fact that photosynthesis was measured instantaneously, whereas grain yield is the result of interplay of many processes, spanning the entire growth period.

g_s bears a positive relationship with P_N, because higher g_s increases CO_2 diffusion into leaves thereby causing higher P_N (Taiz and Zeiger 2002, Ashraf *et al.* 2003). Relationships between g_s and ψ_w have also been drawn in many studies (Bates and Hall 1981, Blackman and Davies 1985, Ashraf and O'Leary 1996, Ashraf *et al.* 2003). Severe plant water deficits either due to drought or salt stress are correlated with suppression of g_s. However, there are contrasting reports regarding the association of g_s with ψ_w. For example, reduction in g_s in cowpea was not related to ψ_w (Bates and Hall 1981, Osonubi 1985). Similarly, a little relationship between g_s and ψ_w or turgor potential was observed in maize (Blackman and Davies 1985). In our study, salt stress caused a marked reduction in ψ_w and g_s of all genotypes, but the salt tolerant and salt sensitive genotypes did not exhibit any consistent pattern with respect to these two attributes of water relations. We found a negative but non-significant correlation between values of ψ_p and DM production or grain yield of 25 wheat genotypes, except between shoot DM and leaf turgor (Table 5). Each genotype performed differently with respect to maintenance of leaf turgor, because in some genotypes no significant increase in ψ_p was observed under salt stress as compared to that in non-saline conditions, whereas the reverse was true in most of the genotypes. Osmotic adjustment under salt stress occurs due to uptake of ions from the soil solution or by accumulation of organic osmotica (Greenway and Munns 1980, Wyn Jones 1981). Under osmotic stress either due to drought or high salt content, it was thought that reduction in turgor potential leads to growth inhibition (Hsiao 1973, Greenway and Munns 1980). But this is not true in view of contrasting findings resulting from many studies. For example, in barley the expanded leaves of salt affected plants had lower turgor potential than in control plants (Thiel *et al.* 1988). However, the reverse

Table 5. Correlation coefficients (*r*) between pairs of growth and physiological attributes of salt stressed plants of semi-dwarf CIMMYT wheats. *,**,*** = significant at 0.05, 0.01, and 0.001 levels, respectively; ns = non-significant. $n = 23$.

A. Correlation on the basis of percent of control values.

Parameter	Grain yield	P_N	E	P_N/E	g_s	C_i	C_i/C_a	ψ_w	ψ_s	ψ_p
Shoot d.m.	-0.058ns	-0.053ns	-0.021ns	0.024ns	-0.016ns	-0.085ns	-0.113ns	-0.085ns	-0.108ns	0.164ns
Grain yield	-	0.200ns	0.095ns	0.242 ns	-0.064ns	-0.117ns	-0.180ns	0.389ns	0.392 ns	-0.042 ns
P_N		-	0.895***	0.922***	0.763***	-0.673***	-0.641***	-0.371ns	-0.046ns	0.045ns
E			-	0.729***	0.815***	-0.570***	-0.554***	-0.336ns	-0.034ns	0.051ns
P_N/E				-	0.697***	-0.683***	-0.682***	-0.393ns	0.012ns	0.067ns
g_s					-	-0.405ns	-0.428*	-0.396ns	0.088ns	-0.123ns
C_i						-	0.949***	0.267ns	-0.185ns	0.071ns
C_i/C_a							-	0.171ns	-0.170ns	0.010ns
ψ_w								-	0.195ns	-0.120ns
ψ_s									-	-0.783***

B. Correlation on the basis of absolute values.

Parameter	Grain yield	P_N	E	P_N/E	g_s	C_i	C_i/C_a	ψ_w	ψ_s	ψ_p
Shoot d.m.	-0.221ns	-0.052ns	0.003ns	0.023ns	0.049ns	0.395ns	0.416*	-0.288ns	0.359ns	0.429*
Grain yield	-	0.026 ns	0.327ns	-0.402ns	-0.075ns	0.151ns	0.232 ns	0.144ns	-0.493**	-0.464*
P_N		-	0.810***	0.583***	0.901***	-0.326ns	-0.265ns	-0.035ns	-0.143ns	-0.095ns
E			-	0.056ns	0.704***	0.098ns	0.196ns	-0.117ns	-0.202ns	-0.103ns
P_N/E				-	0.564***	-0.674***	-0.686***	-0.147ns	0.043 ns	0.104ns
g_s					-	-0.231ns	-0.191ns	-0.043ns	-0.026ns	0.002 ns
C_i						-	0.877***	-0.254ns	0.143ns	0.231ns
C_i/C_a							-	-0.316ns	0.266ns	0.356ns
ψ_w								-	-0.180ns	-0.604***
ψ_s									-	0.891***

was true in different plant species, *e.g.* spinach (Robinson *et al.* 1983), sugar beet (Heuer and Plaut 1989), two *Sorghum* spp. (Yang *et al.* 1990), citrus (Lloyd *et al.* 1987), and *Leptochloa fusca* (Myers *et al.* 1990). In contrast, Ashraf and O'Leary (1996) found in wheat that leaf turgor potential of plants exposed to mild salt stress (125 mol m^{-3}) did not vary significantly from the controls, but in plants subjected to high salt stress (250 mol m^{-3}) there was a considerable decrease in leaf turgor. Munns (1993) summarised the data for leaf turgor of salt sensitive and salt tolerant cultivars/lines of different species. He concluded that salt sensitive cultivars had higher leaf turgor than their salt tolerant relatives. This was ascribed to the reason that perhaps salt sensitive plants are not able to efficiently exclude salts from their roots, as do the salt tolerant ones.

In addition, the concept that g_s in leaves is controlled by turgor has also been questioned (Munns 1993) in view of the findings of Termaat *et al.* (1985) with wheat and barley in which detailed measurements of g_s and water relation parameters were made. Similarly, no significant relationship between g_s and water potential or turgor potential was found in the 25 wheat genotypes examined (Table 5). Likewise, in another experiment with peanut neither ψ_w nor turgor potential initially changed when g_s decreased due to water stress (Blackman and Davies 1985). Similarly, Ashraf and Waheed (1992) could not find any positive relationship between g_s and turgor potential or ψ_w in some lentil lines differing in salt tolerance.

The evidence that turgor does not control growth can be supported by many studies (Itoh *et al.* 1987, Cramer and Bowman 1991, Pritchard *et al.* 1991, Spollen and Sharp 1991, Munns 1993). They found that turgor in elongating tissues is either not affected by water deficit conditions or when it is, there is no relationship between rate of tissue elongation and turgor potential of the cells. However, turgor is essential for growth since it is responsible for employing an extending force causing cell wall expansion. But the rate of cell wall expansion is actually controlled by rheological properties of cell wall (Green *et al.* 1971) and not directly by turgor. Munns (1993) thought that there are other factors that control growth. These factors could be phytohormones, the balance of which in plant probably controls photosynthesis and growth (Poljakoff-Mayber and Lerner 1999).

It is evident from the data for C_i and C_i/C_a that in all the genotypes both the variables remained unchanged under salt stress with respect to controls. This suggests that g_s is not the major factor affecting photosynthesis in all the genotypes under salt stress. Similarly, parallel changes in P_N and g_s were found in drought-stressed sunflower plants in which C_i remained unchanged (Krampitz *et al.* 1984).

A great variation observed in this set of early CIMMYT germplasm of spring wheat could be of considerable practical value. However, the variability in P_N, g_s, and water relation parameters such as ψ_w and ψ_p had no positive association with the differences in degree of salt tolerance observed in the wheat genotypes examined.

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