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Effect of NaCl, water stress or both on gas exchange and growth of wheat

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Abstract

Responses of wheat (*Triticum aestivum* L.) to various concentrations of NaCl and levels of drought were followed. With the rise of NaCl or drought, or NaCl and drought together, growth was retarded. The water content of shoots and roots was mostly unchanged. The chlorophyll and carotenoid contents were increased in plants subjected to salinity or drought or both. Only high salinity level induced a considerable decrease in net photosynthetic rate (P_N) and dark respiration rate (R_D). P_N and R_D were decreased with the decrease of soil moisture content. The content of Na^+ in the shoots and roots of wheat plants increased with increasing salinity or decreasing soil moisture content or both treatments. Considerable variations in the content of K^+, Ca^{2+} or Mg^{2+} were induced by the NaCl, drought or both treatments.

Additional key words: carotenoids, chlorophyll *a*, chlorophyll *b*, dark respiration rate, net photosynthetic rate, transpiration rate.

Introduction

Water deficiency induced by drought and/or salinity could be regarded as one of the major factors that exert considerable alterations in plant growth and metabolism. The degree of these alterations depends mainly on the level of water stress exerted.

It has been reported that better growth of wheat could be attained by increasing available water irrespective of soil salinity (Mashhady *et al.* 1982). Hence we studied the effect of drought and salinity on the growth, pigment contents, net photosynthetic, dark respiration and transpiration rates and mineral composition in wheat.

Materials and methods

Wheat (*Triticum aestivum* L.) was grown in plastic pots with clay and sand (2:1). Perforated plastic tubes were inserted into the soil to help the distribution of water

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and nutrient solution. Five grains were sowed in each pot. One group of pots were subjected to the desired salinity (0, 20, 40, 80 and 160 mM NaCl) and the other group were watered to the desired soil moisture content (80 %, 60 %, 40 % and 20 % field capacity) that were further kept by daily irrigation. Thereafter, the other group of pots were watered to the desired soil moisture content and salinity (80 % field capacity and subjected to 20, 40, 80 and 160 mM NaCl, 60% field capacity and subjected to 20, 40, 80 and 160 mM NaCl and 40% field capacity and subjected to 20, 40, 80 and 160 mM NaCl). At the end of the experimental period (30 d), fresh and dry matter yields of roots and shoots were determined by drying in an aerated oven at 70 °C until constant dry mass. Transpiration rate was measured under 25 °C as described by Bozcuk (1975). The content of chlorophylls *a* and *b* and carotenoids were determined spectrophotometrically (Metzner *et al.* 1965). Net photosynthetic rate (oxygen evolution) and dark respiration rate (oxygen consumption) were determined manometrically using disks (diameter 16 mm) of leaf tissue exposed at 25 °C, irradiance of 5.9 W m^{-2} (40 W *GEF* lamps) using the Warburg buffer *No. 2961* type *VL 85* (Umbreit *et al.* 1959). Sodium and potassium were determined by flame photometer method (Williams and Twine 1960), calcium and magnesium by the versene titration method (Schwarzenbach and Biedermann 1948).

Results and discussion

The transpiration rate was slightly stimulated by 20 and 40 mM NaCl. However at higher NaCl concentration as well as all decreased soil moisture levels the transpiration rate was significantly reduced (Table 1). Salt stress in the root medium strongly retards the availability of water (Hayward and Spurr 1943) in addition to the water movements in the roots (O'Leary 1969) and consequently alters the transpiration of plants (Gale *et al.* 1967, Kaplan and Gale 1972). Camacho *et al.* (1974) suggested that plant species differ in their strategy, some sharply close their stomata in dry air to conserve water at the expense of photosynthesis, others exhibit only moderate humidity response and maintain high photosynthesis in dry air at the expense of high water use.

The fresh and dry matter yields of shoots and roots were reduced with the rise of salinity or decreased soil moisture content. The reduction in growth could be attributed to the reduction in cell division and/or in cell enlargement (Nicholls and May 1963, Slatyer 1967, Terry *et al.* 1971). Also Schwarz (1985) stated that reduced plant growth under water stress conditions has been considered to result from various factors, the most important of which are physiological drought, induced by the low water potential of the soil solution and osmotic adjustment in plants as a result of increased ionic concentration in their cells, which may result in deformation of macromolecules by disrupting their shell of bound water.

The water content of shoots and roots remained unchanged up to the high level of salinity or low level of soil moisture. However, the water content of roots subjected to a combination of salinity and drought was significantly reduced compared with plants subjected to drought stress only (Table 1). Tolerance of the experimental plants closely associated with a relatively stable water content.

Table 1. Effect of different NaCl concentrations (0 - 160 mM), soil moisture contents (80 - 20 % field capacity) or combination of NaCl and soil moisture treatments on transpiration rate, E [mg(H_2O) m^{-2} s^{-1}], fresh and dry mass [g $plant^{-1}$] and water content, w.c. [g g^{-1}(d.m.)] of wheat.

Treatment		E	Shoot			Root		
			f.m.	d.m.	w.c.	f.m.	d.m.	w.c.
Control		12.17	0.574	0.174	2.299	0.142	0.091	0.560
NaCl	20	13.22*	0.584	0.175	2.337	0.131	0.086	0.523
	40	13.03*	0.460**	0.135*	2.407	0.108**	0.070**	0.543
	80	11.49	0.298**	0.094**	2.170	0.085**	0.055**	0.545
	160	7.68**	0.261	0.081**	2.222	0.064	0.041**	0.561
L.S.D.	at 5 %	0.802	0.047	0.032	0.361	0.012	0.011	0.081
	at 1 %	1.257	0.074	0.050	0.567	0.019	0.017	0.128
Drought	80	12.13	0.591	0.132	3.477**	0.154	0.050*	2.080**
	60	9.03**	0.573	0.124*	3.621**	0.130	0.038**	2.421**
	40	7.81**	0.352**	0.083**	3.241*	0.109	0.032**	2.406**
	20	5.32**	0.085**	0.022**	2.864	0.055	0.016**	2.438**
L.S.D.	at 5 %	1.312	0.099	0.044	0.607	0.098	0.032	0.433
	at 1 %	2.057	0.156	0.070	0.952	0.154	0.050	0.679
NaCl	20 + 80	12.44	0.659*	0.153	3.307*	0.164	0.085	0.929**
+	40 + 80	8.12**	0.595	0.136	3.375*	0.138	0.052**	1.654**
Drought	80 + 80	7.96**	0.494*	0.112	3.411*	0.064**	0.026**	1.462**
	160 + 80	6.81**	0.291**	0.066**	3.409*	0.051**	0.017**	1.948**
L.S.D.	at 5 %	0.879	0.056	0.062	1.044	0.047	0.014	0.098
	at 1 %	1.379	0.088	0.097	1.638	0.074	0.021	0.154
NaCl	20 + 60	9.69**	0.538	0.126	3.270*	0.096**	0.041**	1.341**
+	40 + 60	7.89**	0.455**	0.109*	3.174*	0.074**	0.032**	1.313**
Drought	80 + 60	5.95**	0.318**	0.090*	2.533	0.056**	0.024**	1.333**
	160 + 60	2.34**	0.147**	0.042**	2.500	0.030**	0.013**	1.308**
L.S.D.	at 5 %	0.873	0.074	0.065	0.662	0.012	0.017	0.257
	at 1 %	1.369	0.116	0.102	1.039	0.018	0.026	0.403
NaCl	20 + 40	6.01**	0.280**	0.077**	2.636	0.058**	0.031**	0.871**
+	40 + 40	3.24**	0.262**	0.069**	2.797*	0.040**	0.027**	0.481*
Drought	80 + 40	2.12**	0.176**	0.049**	2.592	0.028**	0.023**	0.217**
	160 + 40	1 26**	0.045**	0.012**	2.750	0.024**	0.020**	0.200**
L.S.D.	at 5 %	0.850	0.012	0.011	0.496	0.010	0.009	0.074
	at 1 %	1.333	0.019	0.017	0.778	0.015	0.014	0.116

* - significant at $P = 0.05$; ** - highly significant ($P = 0.01$).

Treatments with salinity, drought or with salinity and drought induced mostly an increase in chlorophyll (Chl) *a*, Chl *b* and carotenoids (Car) contents compared with the untreated plants. NaCl up to 80 mM also stimulated net photosynthetic rate (P_N) and dark respiration rate (R_D). The high concentration of NaCl and the most severe water stress inhibited P_N and R_D (Table 2). Mild level of salinity and drought stimulated only P_N but not R_D. In this context, Ahmed *et al.* (1989) indicated that maize plants tolerated mild salt stress and exhibited higher pigment content compared with the control. The observation that the Chl content was not affected by the drought stress, is in accordance with the findings of Kulshrehtha *et al.* (1987) when two wheat genotypes of differing drought tolerance were subjected to drought stress. In this regard, it is interesting to note that it has been proposed (Mayoral *et al.*

Table 2. Effect of different NaCl concentrations (0 - 160 mM), soil moisture contents (80 - 20 % field capacity) or combination of NaCl and soil moisture treatments on pigment (Chl *a*, Chl *b* and Car contents [mg g^{-1}(d.m.)], net photosynthetic rate, P_N [µmol(O_2) g^{-1}(d.m.) s^{-1}] and dark respiration rate, R_D [µmol(O_2) g^{-1}(d.m.) s^{-1}] of wheat.

Treatment		Chl *a*	Chl *b*	Car	P_N	R_D
Control		10.267	3.599	2.760	198.24	385.46
NaCl	20	9.066*	5.622**	3.310*	1203.12**	296.88**
	40	18.823**	6.088**	5.423**	225.41**	358.61**
	80	21.348**	6.948**	6.155**	194.69	512.42**
	160	16.660**	5.411**	5.571**	131.06**	113.64**
L.S.D.	at 5 %	1.124	0.770	0.430	11.693	11.276
	at 1 %	1.763	1.207	0.674	18.335	17.682
Drought	80	15.205**	5.271*	5.033**	1073.53**	384.12
	60	20.079**	6.796**	5.655**	673.08**	278.57**
	40	22.770**	7.717**	6.827**	403.74**	250.31**
	20	24.589**	6.222**	5.095**	123.33**	238.60**
L.S.D.	at 5 %	1.044	1.537	0.496	12.264	10.604
	at 1 %	1.638	2.410	0.778	19.231	16.628
NaCl	20 + 80	11.201	3.884	3.580*	848.65**	252.61**
+	40 + 80	15.806**	5.466	4.857**	857.56**	245.35**
Drought	80 + 80	19.407**	6.618**	5.641**	1160.19**	206.80**
	160 + 80	19.885**	5.922**	5.661**	954.77**	38.19**
L.S.D.	at 5 %	2.887	0.879	0.820	18.012	10.219
	at 1 %	4.527	1.379	1.286	28.244	16.025
NaCl	20 + 60	20.027**	6.691**	6.000**	734.37**	203.13**
+	40 + 60	20.542**	7.347**	6.204**	722.93**	191.08**
Drought	80 + 60	22.192**	4.806**	5.771**	1174.70**	225.90**
	160 + 60	21.685**	5.510**	3.049	340.00**	250.00**
L.S.D.	at 5 %	2.690	0.694	0.788	19.204	5.778
	at 1 %	4.218	1.089	1.235	30.113	9.061
NaCl	20 + 40	22.564**	7.807**	6.908**	1349.14**	215.52**
+	40 + 40	19.090**	6.603**	5.823**	1135.05**	229.89**
Drought	80 + 40	21.707**	6.714**	5.146**	1156.10**	226.34**
	160 + 40	22.935**	5.818**	5.372**	839.62**	202.85**
L.S.D.	at 5 %	1.811	0.904	0.542	27.230	8.590
	at 1 %	2.840	1.418	0.851	42.700	13.470

* - significant at $P = 0.05$; ** - highly significant ($P = 0.01$).

1981), that chlorophyll stability during drought may be characteristic of drought-tolerant plants, and may therefore be used to differentiate between drought resistant and drought susceptible plants which would enable the breeder to screen for drought resistance.

The reduced photosynthetic activity under high level of salinity has been considered to result partially from reduction in stomatal aperature, even when there is a full osmotic adjustment and pressure potential is high (Schwarz 1985). This

Table 3. Effect of different NaCl concentrations (0 - 160 mM), soil moisture contents (80 - 20 % field capacity) or combination of NaCl and soil moisture treatments on mineral composition (mg g^{-1}(d.m.)] of wheat.

Treatment		Shoot				Root			
		Na	K	Ca	Mg	Na	K	Ca	Mg
Control		29.80	50.36	14.20	2.04	57.50	19.00	15.00	6.12
NaCl	20	28.60	47.20	16.00	2.76	64.40**	20.70	19.40**	7.20*
	40	29.80	50.10	16.60	2.68	66.70**	21.70*	19.20**	3.24**
	80	63.30**	44.00**	16.00	2.16	76.10**	18.00	18.40**	3.12**
	160	65.50**	38.90**	15.40	2.04	87.90**	17.60	16.80*	1.20**
L.S.D.	at 5 %	2.017	3.753	3.154	1.296	3.402	2.643	1.390	0.792
	at 1 %	3.162	5.885	4.946	2.032	5.334	4.145	2.180	1.242
Drought	80	51.00**	50.40	19.60**	5.20**	64.40**	21.20*	15.20	4.56**
	60	54.20**	47.80	16.80*	4.40**	76.10**	21.40*	16.20	4.20**
	40	70.20**	34.90**	15.67	2.16	78.40**	22.40**	21.40**	7.80**
	20	99.67**	32.80**	14.80	1.68	83.67**	28.50**	21.30**	10.92**
L.S.D.	at 5 %	4.955	3.753	2.257	0.516	2.746	1.862	1.386	0.568
	at 1 %	7.770	5.885	3.540	0.809	4.306	2.920	2.173	0.891
NaCl	20 + 80	49.80**	32.30**	14.20	2.52	57.60	19.70	8.60**	7.20**
+	40 + 80	57.60**	39.20**	11.20**	4.92**	71.40**	18.80	11.60**	8.64**
Drought	80 + 80	67.90**	40.80**	8.60**	6.00**	79.60**	19.70	11.40**	8.80**
	160 + 80	75.00**	46.40	8.20**	6.84**	89.00**	19.60	13.60*	9.96**
L.S.D.	at 5 %	4.248	4.100	0.568	0.588	4.031	1.990	1.130	0.542
	at 1 %	6.662	6.429	0.891	0.922	6.322	3.121	1.772	0.851
NaCl	20 + 60	54.30**	43.30**	7.00**	4.56*	60.70*	28.90**	8.60**	16.68**
+	40 + 60	59.90**	46.90	7.80**	5.64**	67.50**	29.50**	8.60**	16.00**
Drought	80 + 60	68.90**	45.00*	9.00**	6.48**	69.10**	19.20	8.00**	11.28**
	160 + 60	65.40**	49.70	9.70**	8.20**	73.70**	16.50*	12.67**	10.80**
L.S.D.	at 5 %	3.735	3.572	1.353	1.765	3.110	2.306	0.543	1.295
	at 1 %	5.857	5.601	2.122	2.767	4.877	3.617	0.852	2.031
NaCl	20 + 40	61.10**	44.00*	8.00**	4.70**	76.00**	33.40**	15.20	7.68
+	40 + 40	85.70**	46.10*	8.80**	5.16**	82.10**	31.60**	16.00	12.12
Drought	80 + 40	116.67**	51.25	12.30*	5.20**	150.83**	44.80**	15.33	14.00
	160 + 40	118.83**	70.67**	13.00	7.80**	152.83**	52.25**	15.50	13.80
L.S.D.	at 5 %	6.757	4.133	1.286	1.286	3.402	1.631	1.835	1.835
	at 1 %	10.596	6.481	2.017	2.017	5.334	2.558	2.877	2.877

* - significant at $P = 0.05$; ** - highly significant ($P = 0.01$)

interferes with CO_2 diffusion into the plant and limitation of photosynthesis by CO_2 concentration. This corroborates the data obtained *e.g.* by Flanagan and Jefferies (1989) who indicated that the lower P_N in plants grown at 200 and 350 mol m^{-3} NaCl were a result of reduced stomatal conductance and low intercellular CO_2 concentration. For wheat leaves Rawson (1986) has shown a larger increase in P_N for a given rise in stomatal conductance under salinity as compared with non-saline conditions, also suggesting that P_N was less sensitive to salinity than transpiration. The increase in P_N at low salinity levels can also be attributed to an increase in chlorophyll concentrations per unit leaf area (Plaut *et al.* 1990). The reduction of growth under salinity conditions could be related to the increase of maintenance respiration (Schwarz 1985), who reported that the energy cost of maintenance is greater under salt stress as a result of requirements for compartmentation and secretion and for repair of cellular damage.

There is a considerable amount of evidence (Huq and Palmer 1978), that drought stress can generate the superoxide radical ($O_2^{\cdot}$) in plant tissues which is converted to hydrogen peroxide (H_2O_2) by superoxide dismutase. The increasing level of H_2O_2 in water stressed tissues has been found to be a function of increasing magnitude of water stress (Mukherjee and Choudhuri 1985). H_2O_2 strongly inhibits CO_2 fixation, possibly by inactivating transketolase (Kaiser 1976) or by inactivating several Calvin cycle enzymes upon reaction with essential sulfhydryl groups (Smirnoff and Colombé 1988). This would seem to have been characterized by a higher efficiency in the drought-tolerant cultivars as during drought-stress the drought-tolerant cultivars are capable of maintaining higher P_N (Van Rensburg and Krüger 1993).

The inhibition of respiration may be due to the interruption in some way or the other of any of the different phases of respiration such as glycolysis, the tricarboxylic acid cycle or pentose pathway, leading to a decrease in respiration activity (Shehata and Hatata 1982).

Sodium accumulation in shoots and roots of wheat plants was stimulated by all the NaCl levels and sodium accumulation increased gradually with the rise of salt level. Most of the investigated salt levels inhibited the accumulation of potassium in shoots and roots and accumulation of magnesium in roots. On the contrary the accumulation of calcium in shoots and roots was slightly stimulated.

The lowering the soil moisture content resulted in a considerable increase in Na^+ and Ca^{2+} accumulation either in shoots or roots and in K^+ and Mg^{2+} accumulation only in roots. The contents of Na^+ in shoots and roots of wheat plants increased with interaction between salinity and soil moisture content. The contents of K^+ remained more or less unchanged. The increase in cation content due to salinity stress should be considered beneficial in osmotic adjustment. Such an osmotic adjustment (Meiri and Poljakoff-Mayber 1969), mainly achieved in the present work by the high content of Na^+, should have been excreted into the cellular vacuoles (Kylin and Hansson 1971) who demonstrated the role played by cation ratio in enzyme activities.

Finally, it should be recalled that the inhibited or stimulated accumulation of mono- and divalent cations, at certain levels of salinity or drought or both salinity and drought, may be one aspect of the role played by cations in regulating some particular reaction or phase of metabolism to overcome the stress (*e.g.* Garcia-Reina *et al.* 1988, Benzioni *et al.* (1992), Hamada and El-Enany (1994).

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