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Growth and gas exchange of wheat under saline and sodic conditions

Ahmad, Manzoor

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GROWTH AND GAS EXCHANGE OF WHEAT UNDER SALINE AND SODIC CONDITIONS

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by

MANZOOR AHMAD
B.Sc. (Honours) Agriculture (UAF)
M.Sc. (Honours) Agriculture (UAF)

School of Agricultural and Forest Sciences
University of Wales, Bangor
Gwynedd, LL57 2UW, UK

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SUMMARY

Research studies reported in this thesis were performed to investigate the effects of salinity and sodicity on gas exchange and growth of different wheat varieties having contrasting salt tolerance. The research was conducted to identify the traits responsible for imparting salt tolerance or salt sensitivity in wheat. Experiments were conducted under saline and sodic field conditions and in greenhouse in solution culture with acidic and alkaline reaction.

There was a broad variation in salt tolerance in various wheat varieties used in different experiments. Salt tolerance mostly depended on the ability of different cultivars to exclude Na^+ and Cl^- and to retain K^+. Different wheat varieties responded differently to salt stress. SARC-1 and Kharchia-65 showed better performance than the salt-sensitive variety Punjab-85 in solution culture as indicated by their ability to maintain higher leaf area, dry weight and relative growth rate, at 150 mol m^{-3} NaCl stress. At 150 mol m^{-3} NaCl stress, hundred grain weight in Kharchia-65 was lower than SARC-1 and PAK-81 although its leaf area and dry weight was the highest. This suggested the presence of some inhibitory mechanism which hindered the translocation of assimilates from the leaves to the seeds at high salinity.

LU26S proved to be the most salt-tolerant variety and gave the highest grain weight per spike under saline and sodic soil conditions as indicated by its lower Na^+ uptake, higher K^+/Na^+ ratio, higher Pn, higher dry weight of shoots and spikes and better grain development (100 grain weight). High Na^+ uptake, lower K^+/Na^+ ratio, lower dry weight of main shoots and spikes and lower 100 grain weight seemed to be the main reasons for salt-sensitivity in Punjab-85.

Punjab-85 which was the most salt-sensitive variety in the glasshouse and saline soil conditions showed medium tolerance to sodicity possibly due to smaller effects on its yield components. Kharchia-65 is a salt-tolerant variety but it did not prove tolerant to sodic conditions indicated by its failure to maintain flag leaf area and dry weight under very dense sodic soil conditions. Pooled data for grain weight per spike for the ten wheat varieties tested under sodic soil conditions showed little correlations with Na^+, K^+ contents of the flag leaves and K^+/Na^+ ratios. Greater uptake of Na^+ and lower uptake of K^+ was noted in the wheat varieties sown in sodic soil than those in the saline soil.

NaCl salinity decreased the rate of net photosynthesis by affecting stomatal and non-stomatal factors. In the salt-sensitive variety, the effect of age seemed to be due to non-stomatal factors which seem to be influenced by excessive concentrations of Na^+ and Cl^- in the leaves.

Fitting a rectangular hyperbola model for Pn/I response curves gave a good fit but the calculated values for Pn_{max} were 32-66% higher as compared to actual observed values. Under salt stress, overall photosynthetic productivity was higher in LU26S than in Punjab-85 as indicated by its higher Pn_{max}, higher α, lower I_c and lower observed R_d, particularly in the older leaves.

The experiment conducted on SARC-1 variety under alkaline pH conditions provided some evidence that the effects of salinity on Pn, growth and uptake of toxic ions are greater at high pH of the growth medium (pH 8.5) than at low pH (pH 5.8). Percentage decreases in most of the growth parameters by salinity, and increases in concentrations of toxic ions (Na^+ and Cl^-) were also greater at high pH than at low pH. These effects were not so severe when the same experiment was repeated with LU26S and Punjab-85 at pH 8.

High salinity caused an increase in Na^+ and Cl^-, and a decrease in K^+, Ca^{2+}, Mg^{2+}, K^+/Na^+ ratio, Zn^{2+}, Fe^{2+} and Mn^{2+}. High pH induced an increase in Na^+, K^+, Cl^-, K^+/Na^+ and a decrease in Zn^{2+}, Fe^{2+} and Mn^{2+}. Generally, weight of grains per plant and 100 grain weight was comparatively greater in LU26S.

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LIST OF ABBREVIATIONS AND SYMBOLS

Ca^{2+} = calcium ion

Ci = sub-stomatal carbon dioxide (Ci; $\mu l\ l^{-1}$)

Cl^- = chloride ion

cm = centimetre

CO_2 = carbon dioxide

DAS = days after sowing

df = degree of freedom

$dS\ m^{-1}$ = deci siemen per metre

E = rate of transpiration ($mmol\ m^{-2}\ s^{-1}$)

EC_e = electrical conductivity of saturation paste extract

Emax = response of infra red gas analyzer to infinite water concentration

EMS = error mean square

ESP = exchangeable sodium percentage

Fe^{2+} = iron ion

g = gram

g_s = stomatal conductance ($mol\ m^{-2}\ s^{-1}$)

ha = hectare

I = photosynthetic photon flux density

I_c = photon flux compensation point

IRGA = infra red gas analyzer

K^+/Na^+ = potassium sodium ratio

K^+ = potassium ion

kg = kilogram

l = litre

LSD = least significant difference

m = metre

me = milliequivalent

meq = milliequivalent

mg = milligram

Mg^{2+} = magnesium ion

Mn^{2+} = manganese ion

mol m^{-3}= mol per cubic metre

Na^{+} = sodium ion

NaCl = sodium chloride

nm = nanometre

NS = not significant

p(0.05) = probability at 5% level of confidence

Pn = rate of net photosynthesis (μmol m^{-2} s^{-1})

Pn_{max} = maximum net photosynthesis

PPFD = photosynthetic photon flux density (μmol m^{-2} s^{-1})

r = coefficient of linear correlation

R_d = dark respiration

RGR = relative growth rate

S = salinity

SAR = sodium absorption ratio

SS = sum of squares

Tl = leaf temperature (°C)

V = variety

v = version

WOG = weight of grains

Zn^{2+} = zinc ions

α = photosynthetic efficiency

°C = degree centigrade

CHAPTER 1

GENERAL INTRODUCTION

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1.1 Nature and Extent of Salinity

Accumulation of excessive salts in the root zone affects plant growth adversely and such soils are classified as salt affected soils. Salinity is wide spread and is an important factor in world agriculture especially in the arid and semi-arid regions. Estimates for the extent of salt-affected land in the world vary a lot and the area has been put variously between 340 and 950 x 10^6 hectares (Flowers *et al.* 1986). The soluble salts that occur in soils consist mostly of different proportions of the cations sodium, calcium, magnesium, potassium and the anions chlorides, sulphates with minor amounts of bicarbonates, carbonates and nitrates. Salt affected soils occur naturally in arid and semi-arid regions of the world (Backlund and Hoppes, 1984). The original and, to some extent, the direct source of all the salts are the primary minerals found in the soil and in the exposed rocks of the earth crust. During the process of chemical weathering , which involves hydrolysis, hydration, solution, oxidation and carbonation, these constituents are gradually released and made soluble. The ocean may be the source of salts in soils where parent material consists of marine deposits that were laid down during earlier geological periods and were uplifted later on. The oceans are also the source of salts in certain low lying areas of the world along the margins of sea coasts. The salts may also be moved inland through the transportation of sea spray by winds. More and more land is being brought under irrigation to feed the ever increasing population of the world. All irrigation waters which are used for irrigation contain varying amounts of dissolved salts. Significant amounts of salts continue to be added to the soil with irrigation water which is also a major cause for soil salinity. The twin menace of water logging and salinity in the Indus basin is one of the major problems related to irrigated agriculture in Pakistan. These two problems are also found in other parts of the world.

Salt affected soils are classified in different classes according to the nature and severity of the problem.

1.1.1 Saline soils

Soils containing abundant amounts of soluble salts which can hinder the germination and growth of most crop plants, but not containing enough exchangeable sodium to affect the soil properties are called 'Saline soils'. The electrical conductivity of the saturation extract (EC_e) of saline soils is 4 or more than 4 dS m^{-1}, and the exchangeable sodium percentage (ESP) is less than 15. The pH of the saturated paste is less than 8.5. These soils are generally recognized by the presence of a white salt crust on the surface. These soils have a good structure and are well flocculated. Their permeability to water is either greater than or equal to that of similar non-saline soils.

1.1.2 Saline-sodic soils

With increase in soil pH and salt concentration due to evaporation from the bare surface, there is a tendency for calcium and magnesium in the soil solution to precipitate as carbonates and sulphates. The precipitation of these soluble salts increases the proportion of sodium in the soil solution and consequently there is an increase in the amount of exchangeable sodium on the soil exchange complex. Such soils have an ESP of 15 or more and an EC_e of more than 4 dS m^{-1}. The pH is usually greater than 8.5. In the presence of excess soluble salts their appearance is similar to those of saline soils. Soluble salts tend to flocculate soil particles, while exchangeable sodium tends to disperse and deflocculate the soil and thus decreases its permeability to air and water. In these soils, the plants suffer due to osmotic effects as well as toxic effects of sodium.

1.1.3 Sodic soils

Soils containing sufficient exchangeable sodium to affect its physical and chemical properties, seedling emergence and plant growth adversely but not containing appreciable quantities of soluble salts are called sodic. The ESP of sodic soils is 15 or more and the EC_e is less than 4 dS m^{-1}. The pH is usually greater than 8.5. Since the soils are generally dispersed; infiltration, drainage and aeration are poor. Because of dispersed soil condition, it becomes difficult to maintain good tilth for optimum seed germination, seedling emergence and plant growth. Because of low infiltration it also becomes rather difficult to replenish the water supply in the root zone by irrigation.

1.1.4 Extent of Salt-affected and Waterlogged soils in Pakistan

There is a lot of controversy about the extent of salt-affected soils reported by various agencies in Pakistan (Muhammed, 1981), especially the ones that fall within the culturable canal command area (Mian and Ali, 1980). According to one estimate (Muhammed, 1993), about 5.7 million hectares of land is affected by salinity in irrigated areas of Pakistan (Table 1.1) which constitutes about 39% of the total irrigated area (14.3 million hectares) of the country. According to another estimate by the Water and Power Development Authority (WAPDA), about 30% of the irrigated area of the Indus basin is affected by different levels of surface soil salinity.

Table 1.1: Extent and categories of salt-affected soils (1000 ha)

Province	Saline	Saline-sodic		Sodic	Total	Gypsiferous Saline-sodic
		Permeable	Impermeable			
Punjab	504.4	1225.3	856.5	-	2586.2	57.2
%	19.5	47.4	33.1	-	100.0	2.2
Sind	1342.3	673.1	277.6	28.2	2321.2	339.1
%	57.8	29.0	12.0	1.2	100.0	18.9
NWFP	501.6	5.2	9.2	-	516.0	6.2
%	97.2	1.0	1.8	-	100.0	1.2
Baluchistan	175.0	125.0	4.4	-	304.4	90.0
%	57.5	41.4	1.4	-	100.0	29.6
Pakistan	2523.3	2028.6	1147.7	28.2	5727.8	492.5
%	44.1	35.4	20.0	0.5	100.0	8.6

Source: Compiled from Soil Survey of Pakistan reports (1967-79) by Muhammed (1983).

The performance of crop plants is expected to be different under different types of salt stresses. Crops need to be evaluated regarding their performance under these conditions for proper utilization of the vast salt affected areas of the world for food production.

A lot of research work has been done in Pakistan and else where for better crop production from salt-affected lands. The strategy of selection of salt-tolerant crops is a comparatively recent approach in this regard.

Different approaches have been made to tackle the problem of salt-affected soils. Efforts have been made to reclaim these soils by leaching (saline soils) or by leaching in combination with appropriate chemicals (saline sodic and sodic soils), provision of proper drainage and adopting suitable biological approaches (Richards, 1969; Flowers et al. 1977; Oster *et al.* 1984; Maas, 1984, 1986; Qureshi *et al.* 1993). The biological approach is comparatively recent and currently, a lot of research work is being done to investigate different aspects of responses of plants to environmental stresses. Wheat is the most important and extensively grown cereal crop in the world, hence it was selected for the studies reported in this thesis.

1.2 Importance of Wheat in Pakistan

Wheat is the main staple food crop in many parts of the world including Pakistan. The agricultural economy of Pakistan is dominated by relatively few crops, primary among them being wheat. In 1987-88, about 7.7 million hectares were under wheat which gave a grain yield of about 14.4 million metric tonnes (Government of Pakistan, 1988). In spite of this yield, domestic needs are often met through imports from other countries. According to another estimate, wheat cultivation encompassed roughly 54% of the national area devoted to crop production in 1992/93, and has no substantial competitor during its winter growing season (Shean, 1993). Total wheat output in 1993/94 was approximately 15.5 million metric tons. Its importance becomes more evident when we find that a major portion of rice production which could be consumed as food, is exported to earn foreign exchange.

Population of Pakistan was 124.4 million in 1994 (Government of Pakistan, 1996). Current population of the country is estimated to be 140 million people, which is growing at a very fast and alarming rate of 2.9% and is among the highest in Asia. The projected population for the year 2020 is 262 million when it will rank as the fifth largest nation in the world. To feed this ever increasing population, the government is facing a continuous challenge for improving the basic infrastructure for sustained agricultural production. To cope with the food requirements of increasing population, output per unit area has to be increased. As good agricultural land and good quality irrigation water are limited, there is only one option to bring the salt-affected areas under cultivation, by using irrigation waters of marginal quality.

1.3 General Effects of Salts on Plant Growth

Salinity causes stunting of plants (Bernstein, 1975) and their colour may change to dark green as compared to the plants growing under normal conditions (Marschner, 1986). Leaves are smaller, though they may be thicker than those of normal plants (Bresler *et al.* 1982). There is often a reduction in the root and shoot growth, leaf area, tillering and biomass production (Kemal-ur-Rahim, 1988; Iqbal, 1992, Ahsan, 1996). The number of effective or productive tillers (ear bearing tillers) have been reported to be decreased seriously by salt stress (Haqqani *et al.* 1984). Responses of cereals to salt stress differ at different growth stages and according to the time, duration, intensity and type of the stress. Plant growth has been reported to be affected by type of salinity (dominated by Cl^- or SO_4^-) and the duration of exposure to it (Marschner, 1986). Salinity affects the growth and expansion of individual leaves rather than reduction in the rate of production of the new leaves (Terry and Waldron, 1984; Iqbal, 1992). The number of leaves and leaf area are decreased indirectly by salinity through decrease in the number of tillers per plant. A reduction in leaf area limits the yield by limiting the area available for photosynthesis (Wyn Jones and Gorham, 1989). Photosynthesis in plants growing in saline media, may also be decreased through increased salt concentration in the leaves which results in accelerated senescence.

1.4 Effects of Salinity and Sodicity on Wheat Growth

Wheat is classed as a moderately salt tolerant crop (Richards, 1969; Bresler *et al.* 1982; Maas, 1984) and its yield starts to be affected above an EC of 6 dS m^{-1}. It is also reported to exhibit a certain degree of tolerance to sodic conditions (Bresler *et al.* 1982) but its growth is stunted at an ESP of 40-60 which is mostly due to adverse physical conditions of the soil. Salt tolerance in crops such as wheat and barley is largely determined by their ability to exclude sodium and Cl^- from their shoots and their ability to maintain high shoot K^+ concentrations. This implies the operation of transport processes which discriminate against Na^+ and for K^+ (Gorham, 1994). Kirkby and Mengel (1967) reported that changes in pH of the nutrient medium and the type of nitrogen supplied affected the ion uptake of plants.

The ability of the wheat crop to tolerate moderate levels of salinity at germination and emergence has been well documented but the physiological mechanisms of salinity tolerance are not so clear (Kemal-ur-Rahim, 1988). Considerable increase in sodium contents of wheat plants grown in salt-affected soils or in solution culture containing NaCl, have been reported by many workers (Gorham *et al.* 1986; Sharma, 1989; Kingsbury and Epstein, 1986; Azmi and Alam, 1990; Padole, 1991; Salim, 1991; Gill *et al.* 1992). Salinity also causes an increase in chloride content of the wheat leaves (Kingsbury and Epstein, 1984, 1986; Rawson, 1986). Excessive Na^{+} in the sodic soil may exert important secondary effects on plant growth through adverse structural modifications of the soil.

Reduced uptake of Zn^{2+}, Mn^{2+} and Fe^{2+} were reported by salinity and/or sodicity stress in wheat (Padole, 1991). In a pot study, Srivastava and Srivastava (1993) found that as soil pH increased from 7.2 to 10.3, levels of water soluble and exchangeable Fe^{2+} decreased while levels of iron oxides increased. Internal concentration of above mentioned micronutrients considered adequate for most of the crop plants are 20 mg/kg for Zn^{2+}, 100 mg/kg for Fe^{2+} and 50 mg/kg for Mn^{2+} in dry weight (Salisbury and Ross, 1991).

1.5 Osmotic Effects on Leaf Growth

There is ample evidence to prove that an increase in osmotic pressure of the soil solution results in a decrease in water uptake by the plant roots (Richards, 1969). In addition to this, soil moisture tension increases as the soil becomes drier and this negative effect is apparently additive to the osmotic pressure. Delane *et al.* (1982) and Munns *et al.* (1982) also proposed that water deficit caused by salinity stress in the expanding tissues was responsible for a reduction in growth. Leaf cell turgor has been described as a major factor influencing plant growth (Hsiao, 1973). During stress, water potential of both leaves and spikelets are reduced in wheat and leaf turgor may approach zero (Morgan, 1980). Termaat *et al.* (1985) applied pneumatic pressure to the roots to raise the turgor of the leaves and concluded that shoot turgor alone was not regulating the growth of the NaCl affected plants. They further postulated that a message coming from the roots may be responsible for regulating the growth of the shoot. Munns and Termaat (1986) reported that leaf growth is more sensitive to salinity than root growth. In salt stressed plants, growth reduction occurs in two phases (Munns *et al.* 1995) . In the first phase, growth is reduced by osmotic strength of the salt solution outside the roots, and thus affects all genotypes similarly. The second phase would start only after salt had accumulated to toxic levels which may cause injury and hence reduce the supply of assimilates to the growing regions. Genotypic differences in growth are seen during this second phase.

1.6 Specific Ion Effect

The influence of excessive concentrations of salts on plant growth is an extremely complex subject and involves many fundamental principles of plant nutrition (Richards, 1969; Bresler *et al.* 1982). Salinity at non-toxic levels may suppress leaf growth without any apparent injury (Rawson and Munns, 1984). On the other hand, it has also been reported that sodium and chlorides when present in relatively small concentrations, may stimulate the productivity of certain crops (Richards, 1969). The specific effects of salinity on the leaf growth could be due to excessive transport of Na^+ or Cl^- to the shoot, excessive transport of other ions such as phosphates or inadequate transport of other ions e.g. K^+, Ca^{2+}, Mg^{2+}, NO_3^- or SO_4^{2-} (Termaat and Munns, 1986). Munns and Termaat (1986) suggested that nitrogen supply could be lower after exposure to NaCl, as Cl^- inhibits NO_3^- uptake. They further reported that carbohydrates accumulate after exposure to salinity but rates of protein synthesis are decreased in NaCl treated plants. In salt tolerant plants such as barley, roots can regulate the rate of salt transport in the xylem (Munns, 1985). Aswathappa and Bachelard (1986) also reported that apart from the general osmotic effects, the prevalence of certain ions such as Na^+, Cl^-, SO_4^{2-}, Mg^{2+}, borates and bicarbonates can be toxic to plants and the high pH often found in salt affected soils can induce Fe and other micronutrient deficiencies. Of the various solutes found in cell sap of mesophtes, K^+ is known to be a major component of the osmotic potential and to play an important role in osmotic regulation of elongating cells, as well as cells with specialised functions such as stomatal guard cells and motor cells (Morgan, 1992).

1.7 Salinity Effect on Gas Exchange in Wheat

Biomass production in plants depends on the accumulation of carbon products through the process of photosynthesis. In wheat under field conditions, net photosynthetic rate varies between 12-32 μmol CO_2 m^{-2} s^{-1} at 680-2200 μmol m^{-2} s^{-1} PPFD in various leaves (Rawson, 1986; Kemal-ur-Rahim, 1988; Iqbal, 1992). Respiration is important for synthesis of new material and maintenance of tissues (King and Evans, 1967) and about half of the carbon assimilated during growth of a wheat plant is respired.. During vegetative development, photosynthates produced by early formed leaves, are partitioned predominately to emerging leaves, tillers and roots (Rawson and Hofstra, 1969), and spike growth both before and after emergence from the boot is supported mostly by photosynthates from the upper two or three leaves on the wheat plant. As growth cannot proceed for long without carbon, changes in patterns of photosynthesis and respiration should reflect the responses of growth to salinity (Rawson, 1986).

Different physiological processes are involved to account for the reduction in yield due to salinity in different crop species (Flowers *et al.* 1986; Kingsbury and Epstein, 1986; Munns and Termaat, 1986) and reduction in photosynthesis is usually related to decreased growth caused by salinity. The effect of salt stress on photosynthesis in wheat is caused mostly due to increases in stomatal and mesophyll resistance (Kingsbury *et al.* 1984; Lawlor, 1976; Rawson, 1986).

Incident light intensity (PPFD) influences both rate and the PPFD at which light saturation of photosynthesis occurs in wheat and other crops (Singh *et al.* 1974). Plants grown at higher PPFD have higher net photosynthesis rate per unit leaf area (Singh *et al.* 1974; Winzeler, 1978; Marshall and Biscoe (1980b); Kaiser, 1984; Iqbal, 1992). Higher light intensities stimulate the increased synthesis of leaf material, including photosynthetic enzymes (Singh *et al.* 1974). High salt concentrations in the cytoplasm on the other hand may damage enzymes and organelles (Läuchli and Epstein, 1984). Leidi *et al.* (1991b) reported a decrease in chlorophyll concentration in the leaves of wheat with increase in pH of the culture medium containing NaCl.

There have been conflicting reports regarding the effects of NaCl salinity and high pH on the gas exchange in wheat. Some workers have found that photosynthesis expressed on a unit area basis was not affected by salt concentrations up to 100 mol m^{-3} NaCl in wheat (Kemal-ur-Rahim, 1988; Leidi *et al.* 1991b). Contrary to these findings, there are numerous reports which show that photosynthesis of wheat is decreased by NaCl stress (Terry and Waldron, 1984; Rawson, 1986; Zerbi *et al.* 1991; Bethke and Drew, 1992; Iqbal, 1992). Decreases in Pn and E in barley cultivars due to NaCl stress were also reported by Kalaji and Nalborczyk (1991) but effects of high sodicity on Pn in two wheat genotypes were non-significant (Khan, 1996) . Yeo *et al.* (1985) and Yeo *et al.* (1991) found a rapid reduction in net photosynthesis in rice leaves due to accumulation of NaCl in the plants grown under saline conditions. Decreases in Pn by NaCl stress have also been reported by Downton (1977) in grapevines, Walker *et al.* (1982) in citrus, Terry and Waldron (1984) in sugar beet and, Bethke and Drew (1992) in capsicum, Heuer and Feigin (1993) in tomatoes and He and Cramer (1996) in *Brassica* species. In certain cases however, Pn even increased at 100 mol m^{-3} NaCl and a decrease was noted only at 150 - 200 mol m^{-3} NaCl stress (e.g. Khan, 1996).

1.8 Brief Review of Research on Salinity and Sodicity Management

Because of the widespread occurrence of these problem soils in Pakistan and other parts of the world, these have been the subject of much research by agronomists, soil scientists, plant physiologists and breeders. These scientists have studied their genesis, physical and chemical properties (Brinkman and Rafiq, 1971; Rafiq, 1975; Bresler *et al.* 1982; Rafiq, 1993; Muhammed, 1993; Sharma, 1993a), appropriate methods of reclamation (Richards, 1969; Oster *et al.* 1984; Ahmad, 1993; Ahmad *et al.* 1993; Sharma, 1993b; Singh, 1993), use of fertilizers for better crop production from salt affected soils (Ali *et al.* 1988; Hussain *et al.* 1991; Leidi *et al.* 1991; Cassman *et al.* 1992; Bajwa, 1993; Bandyopadhay and Singh, 1993; Hawkins and Lewis, 1993; Jilani *et al.* 1993; Zaidi *et al.* 1994). Concerning crop plants, workers have tried to investigate the mechanisms of salt tolerance in different halophytes and non-halophytes and have compared the salt tolerance of different crops (Flowers *et al.* 1977; Kingsbury *et al.* 1984; Läuchli and Epstein, 1984; Cramer *et al.* 1985; Gorham *et al.* 1985; Neumann *et al.* 1988; Austin, 1989; Krishnamurthy and Bhagwat, 1990; Ashraf *et al.* 1991; Pheloung and Siddique, 1991; Salim, 1991; Iqbal, 1992; Noble and Rogers, 1992; Mandal, 1993; Qadar, 1993; Qureshi *et al.* 1993; Reggiani *et al.* 1995; Salama *et al.* 1994; Gorham *et al.* 1994; Gorham, 1994; Munns *et al.* 1995) and attempted to breed new varieties with increased salt tolerance (Ashraf and McNeilly, 1991; Flowers and Yeo, 1995; Ahsan, 1996; Khan, 1996).

1.9 Objectives of the Current Studies

Soil salinity is adversely affecting crop production in arid and irrigated areas of Pakistan and elsewhere in the world. Wheat accounts for nearly a quarter of world's food requirements (Iqbal, 1992), hence its per unit area production has to be increased to cope with the needs of increasing population. One of the possibilities for increasing the productivity is from salt affected soils which are lying un-utilized. Apart from reclamation which is a very expensive option, one option available to farmers is the use of salt-tolerant crops. There is a wide variation in salt tolerance in crop plants to salinity and/or sodicity. Salt tolerance in crop plants mostly depends on their ability to exclude the toxic ions and to retain the beneficial elements. Wheat is a moderately salt-tolerant crop and lot of research work is in progress to improve its salt resistance for getting better yields from the salt affected areas.

Saline and sodic soils have a lot of spatial variability (Shannon and Qualset, 1984;

Richards, 1992; Igartua, 1995), hence salt tolerance is mostly assessed by growing plants in salinized nutrient solutions so that their root zone can be kept at a constant salt concentration. These growing conditions may be suitable for aquatic or marsh plants (Igartua, 1995) but they are not representative of the conditions under which plants grow under their natural or agricultural habitats. Hence these may lead to misleading conclusions and the formulation of inappropriate selection criteria to genetically improve productivity in saline or sodic soils. Considerably less work has been conducted on the combined effect of salinity and high pH in solution culture and under field conditions. Keeping the above limitations in view, the research work reported in this thesis was undertaken to achieve the following objectives.

- To evaluate the effects of different levels of salt stress on some wheat cultivars having varying degrees of salt tolerance with respect to their growth and yield under a uniform and similar set of saline growing conditions.
- To carry out an evaluation of agronomic characters which render a variety tolerant or sensitive and to examine the relationships between stress, leaf area, dry matter, grain yield and other yield parameters.
- To compare and study the yield potential of different wheat varieties under 'saline' and 'sodic' soil conditions, and different ion concentrations in the flag leaves and to correlate these with the yield and yield components of the different varieties.
- To identify factors responsible for imparting salt tolerance in wheat.
- To investigate the responses of wheat to salinity and/or sodicity simultaneously under field and greenhouse conditions and to see whether the experimental results under greenhouse conditions can, with a certain degree of confidence, represent the responses under actual field conditions, which are characterized by spatial variability, high temperatures and humidity with a lot of variability.
- To study the gas exchange response curves of two wheat varieties having variable degrees of salt tolerance (LU26S as salt tolerant and Punjab-85 as salt sensitive variety); under stressed and non-stressed conditions on leaves of different age.
- To test the hypothesis that accumulation of ions in the leaves with increasing age results in a decrease in net photosynthesis and that this decrease is greater in a sensitive variety than in a tolerant variety.

CHAPTER 2

EFFECTS OF SALINITY ON GROWTH AND YIELD OF WHEAT VARIETIES DIFFERING IN SALT TOLERANCE

CHAPTER 2

EFFECTS OF SALINITY ON GROWTH AND YIELD OF WHEAT VARIETIES DIFFERING IN SALT TOLERANCE

2.1 INTRODUCTION

Wheat cultivars have been reported to differ considerably in their tolerance to salt stress (Sharma, 1991; Qureshi *et al.* 1993). Watanabe *et al.* (1992) reported that differences were found in the changing patterns of relative growth rate (RGR) in different species of crops to NaCl concentration in culture solution and the changes in RGR were mainly due to those in net assimilation rate. Kharchia-65 has often been reported to tolerate salt stress better than many other wheat varieties (Kingsbury and Epstein, 1984; Rawson *et al.* 1988; Srivastava *et al.* 1988). Qureshi *et al.* (1993) conducted a series of experiments in solution culture and saline field conditions and have classified different wheat cultivars according to their degree of salt tolerance into tolerant, moderately tolerant, moderately sensitive and sensitive. PAK-81 variety of wheat has been classified by them as moderately salt-tolerant. SARC-1 has also been categorized as a wheat cultivar having moderate salt tolerance (Qureshi, 1993; Personal communication). Ashraf and McNeilly (1991) have reported Punjab-85 as a salt sensitive wheat variety.

It is generally observed that plant Na^+ and Cl^-contents increase and K^+ contents decrease with increasing NaCl concentration. Munns and Termaat (1986) argued that when the non-halophytes grow under saline conditions, ion concentration will eventually build up to toxic levels in the older leaves resulting in their death. The concentration at which this occurs will depend upon the ability of the species to compartment the salts in the vacuoles, and the time it takes to happen will depend mainly on the salinity level, the ability of the roots to exclude salts, and the ambient conditions affecting the rate of transpiration. Munns (1992) concluded that in wheat and barley, chemicals sent from the roots in the transpiration stream could control leaf expansion, and that the xylem sap from plants in dry or saline soil could contain increased amounts of a growth inhibitor, or decreased amounts of a growth promoter of some unknown identity.

The purpose of this study was to evaluate the effects of different levels of salt stress on some wheat cultivars having varying degrees of salt tolerance with respect to their growth and yield under a uniform and similar set of saline growing conditions. It was also intended to carry out an evaluation of agronomic characters which render a variety into a tolerant or a sensitive variety. Another objective of the experiment was to investigate the effects of salinity on leaf area and dry matter at different growth stages and on final grain yield and yield parameters; and to examine the relationships between stress, leaf area and other agronomic characters.

2.2 MATERIALS AND METHODS

2.2.1 Experimental Material and Green House Conditions

The experiment was conducted at Pen y Ffridd field station, University of Wales, Bangor in an environmentally controlled green house at 20/18 °C ±2 ° day/night temperatures and a day length of 16 hours maintained with supplementary light from 400 watt high pressure sodium lamps.

Four wheat varieties having variable degree of salt tolerance were selected which are given below.

VARIETIES	REPORTED SALT TOLERANCE
1. Kharchia-65	Salt tolerant
2. SARC-1	Moderately tolerant to tolerant
3. PAK-81	Moderately tolerant
4. Punjab-85	Salt sensitive

The plants were grown in plastic cells (in plastic trays: P84, Plantpak Ltd. Maldon, Essex, UK) placed over 25 litre capacity plastic tubs (W6-Mailbox International Ltd. Stalybridge, Cheshire, UK). Each tub was fitted with an aeration system for continuous aeration of the nutrient solution. The cells were filled with John Innes No. 1 compost for sowing the seeds. Twenty one seeds of each variety (three adjacent rows with seven seeds/row) were sown in each pot, and the varieties were allocated to each pot randomly.

2.2.2 Sowing of the Seeds

The seeds were sown on July 2, 1993. One seed was sown in each compost-filled notch. The experiment was laid out according to randomized complete block design with two replications.

2.2.3 Nutrient Solution

The plants were grown in solution culture using Phostrogen as a source of macronutrients and modified Long Ashton nutrient solution as a source of micronutrients. Phostrogen (Corwen, Clwyd, UK) is a blended 10-10-27 NPK fertilizer in powder form which also contains 3.6% Ca, 1.3% Mg, 0.4% Fe and 0.02% Mn (Appendix - B). It was applied at the rate of 1.0 g/litre for full strength nutrient solution. Micronutrients were added according to the Long Ashton formula. The hydroponic medium consisted of tap water only for the first 10 days up until the time when the seeds had germinated. During the next three weeks of growth, half strength nutrient solution was used. After that, full strength nutrient solution was used up to the maturity of the crop. The full composition of this nutrient solution is presented in Appendix - A.

2.2.4 Salt Stress

The stress levels in this experiment and others were created by adding commercial NaCl to the nutrient solution, as this is the most common salt found in the saline soils (Munns and Termaat, 1986). There were four salinity levels and two pots at each stress level. The salinity levels used were:

i. 0 mol m^{-3} NaCl (control)

ii. 50 mol m^{-3} NaCl

iii. 100 mol m^{-3} NaCl

iv. 150 mol m^{-3} NaCl.

Salt stress was introduced at 30 DAS according to the treatment levels and was given in increments of 25 mol m^{-3} NaCl per day, being delayed to achieve a uniform stand in all the varieties.

2.2.5 Maintenance of the Experiment

Nutrient solutions were changed after every 15 days along with respective stress levels made with NaCl. Nutrient solution was prepared in bulk in a big portable plastic tank and was added to each pot at the rate of 25 litres per pot. The required amounts of NaCl were weighed and dissolved in the respective pots. The pots were topped up with tap water on alternate days to replace losses through evapotranspiration.

The crop suffered a mild attack of aphids and mildew during its growth. The plants were sprayed twice during the course of the experiment with Benlate (a wettable powder containing

50% W/W benomyl) at the rate of 3.5g per 5 litre of water to control powdery mildew. Fumigation of the green house was done at weekly intervals.

2.2.6 Growth Measurements

A total of five plants were randomly sampled from the two replicates of each treatment. The plants were harvested every 15 days from each treatment and variety starting 15 days after introducing the plants to salinity. The following data were recorded.

a. Total leaf area

Length and width measurements of all the leaves of the harvested plants were recorded at three intervals of 15 days each i.e. 45, 60 and 75 DAS. The leaf area was calculated by using the formula used by Robson and Sheehy for swards (1980) i.e.

Leaf area=(0.9 x Length) x (0.5 x Width)

This formula was used due to non-availability of leaf area meter at the time of measurements and was used for wheat keeping in view of the similarity of leaf shape of swards to wheat (Hollington, P. A. 1993; Personal Communication)

b. Dry weight of plants

After recording the length and width of the leaves, all the shoots and leaves from each plant were dried to a constant weight by placing them in an oven at 70° C for 72 hours. The material was then weighed and dry weight recorded.

c. Relative growth rate

The relative growth rate over the period 45 to 75 DAS was calculated from dry weights per plant using the following equation (Coombs *et al.* 1985).

Relative Growth Rate (R) = {ln(W2) - ln(W1)}/t2-t1

where W1= Initial dry weight of the plant at t1 (45 DAS)

W2= Final dry weight of the plant at t2 (75 DAS)

Ten plants were sampled randomly from each treatment and variety at the time of final harvest and the following data were recorded.

d. Height of the main shoot from base of the stem to spike apex and the length of main spikes.

e. Weight of main shoots and ears

The main shoots and ears from each plant were dried to a constant weight in an oven at

70° C for 72 hours. The material was then weighed and dry weight recorded.

f. Total number of tillers and ears

The number of total tillers and ears were recorded from ten plants from each variety and stress level at the time of the final harvest.

g. Number and weight of grains in main shoot ears

After recording the length and weight of the main shoot ears, these were threshed manually. The grains were counted and their dry weights were recorded.

h. 100 grain weight

2.2.7 Visual Observations

Germination occurred earlier in Kharchia-65 than in the other varieties and later in PAK-81 and Punjab-85. Some seeds in PAK-81 and Punjab-85 did not germinate and resowing was done. Leaf tip burning was noted in all the varieties on August 10, 1993 in the stressed treatments at 100 and 150 mol m^{-3} NaCl. There was no such effect in control and 50 mol m^{-3} NaCl.

Ear emergence started on August 16, 1993 (45 DAS) in 100 and 150 mol m^{-3} NaCl treatments. Tip burning was also observed at 50 mol m^{-3} NaCl at this time. On August 17, 1993, it was noted that in certain plants, some central new leaves on the secondary tillers had died in all the varieties at 100 and 150 mol m^{-3} NaCl. Kharchia-65 produced a lot of foliage and lodging occurred in the control and at 50 mol m^{-3} NaCl at 50 DAS.

At 150 mol m^{-3} NaCl all the varieties matured early and final yield was recorded on September 24, 1993 in this treatment. In other treatments yield data was recorded 3 weeks later.

2.2.8 Statistical Analysis

Statistical analyses i.e. analyses of variance, means, standard errors and correlations were calculated using Minitab statistical package version 10.2 for Windows. Analyses of variance were computed assuming each individual plant was a replicate. Hence there were 5 (for growth analysis data) and 10 (for final harvest data) values for each treatment and variety for each observation. The examples of anova are presented in Appendix 2.1 and 2.2. LSD was calculated by the following equation.

$$LSD = ((2*EMS)/n)^{1/2})*t_{df}$$

n = Number of observations to calculate a mean

t_{df} = Tabulated t value at error degrees of freedom

2.3 RESULTS

2.3.1 Significance of Main Effects and Interactions

To determine the effects of variety and salinity on growth at different stages, an initial anova was computed for leaf area and dry matter by combining the data recorded at 45, 60 and 75 DAS.

The effects of age, salinity and variety were highly significant for leaf area (Table - 2.1). Age x variety and age x stress interactions were also significant. Variety x stress and age x variety x stress interactions were however found to be non-significant.

For dry matter (Table - 2.2), the effects of age, salinity, variety and age x stress were highly significant while age x variety, variety x stress and age x variety x stress interactions were non-significant.

For total number of tillers and ears per plant (Tables - 2.7 & 2.8 respectively), the effects of stress and variety were highly significant. The stress x variety interaction was also significant in both these parameters.

In the case of grain yield and yield components (Table - 2.10) recorded at maturity, the effects of salinity and variety were highly significant for all the measured parameters. The salinity x variety interactions were significant for number and weight of grains but not for 100 grain weight.

In the anova, the observation that the variety x salinity interaction was non-significant for leaf area, dry weight and grain yield indicates that all varieties responded in a similar way to salinity. However, an examination of the results showed that Kharchia-65 and SARC-1 (the salt-tolerant varieties) were able to maintain higher leaf area and dry matter than the other two varieties at 100 and 150 mol m^{-3} NaCl. Dry matter of Punjab-85 was however slightly higher than SARC-1 at 100 mol m^{-3} NaCl. Grain yield per plant was also higher in SARC-1 and Kharchia-65 and lowest in Punjab-85 at 150 mol m^{-3} NaCl.

2.3.2 Leaf Area

Leaf area per plant was recorded in cm^2 and is presented in Table-2.1. In general, there was an increase in leaf area at the second harvest in all the varieties and at all the stress levels and then a decrease at the third harvest. At the time of the first and second harvests, leaf area of Kharchia-65 was the highest at all the stress levels as compared to the other varieties. This trend was not evident at the third harvest when leaf area was highest in SARC-1 at all the stress levels

Table -2.1: Leaf area per plant (cm^2) in different wheat varieties at different salinity levels (mol m^{-3} NaCl).

Varieties	Harvest	Control		50 mol m^{-3}		100 mol m^{-3}		150 mol m^{-3}	
		Means	± SE	Means	± SE	Means	± SE	Means	± SE
Kharchia-65	45 DAS	245	19.0	186	22.7	176	10.0	175	9.4
	60 DAS	455	47.0	358	41.2	227	30.0	108	19.2
	75 DAS	200	43.6	199	55.6	137	31.9	116	15.1
SARC-1	45 DAS	129	15.1	154	27.1	142	24.1	108	11.2
	60 DAS	331	69.9	202	39.6	127	22.3	87	27.8
	75 DAS	234	41.9	184	27.6	146	32.2	132	19.6
PAK-81	45 DAS	145	26.3	117	11.0	101	18.2	100	16.7
	60 DAS	282	24.1	248	35.6	110	22.5	103	18.4
	75 DAS	181	12.7	151	22.8	81	7.3	74	14.3
Punjab-85	45 DAS	143	23.9	108	13.6	97	14.7	89	6.9
	60 DAS	296	34.4	155	21.5	107	21.3	96	18.4
	75 DAS	135	13.0	139	12.8	120	13.6	53	7.0

Means for sampling dates

45 DAS	138.7 ± 0.78
60 DAS	206.6 ± 0.80
75 DAS	142.3 ± 0.78

Means for salinity stress

0 mol m^{-3} NaCl	231.4 ± 1.0
50 mol m^{-3} NaCl	182.9 ± 1.1
100 mol m^{-3} NaCl	130.9 ± 1.0
150 mol m^{-3} NaCl	104.7 ± 1.1

Varietal means

Kharchia-65	216.0 ± 1.0
SARC-1	165.1 ± 1.1
PAK-81	141.1 ± 1.0
Punjab-85	127.8 ± 1.0

Continued on next page ....

Table - 2.1: Leaf area .... (continued from previous page)

Means for age x salinity

	0 mol m^{-3} NaCl	50 mol m^{-3} NaCl	100 mol m^{-3} NaCl	150 mol m^{-3} NaCl
45 DAS	165.6 ± 3.1	141.4 ± 3.2	130.1 ± 3.1	117.6 ± 3.3
60 DAS	341.1 ± 3.1	240.6 ± 3.2	141.5 ± 3.3	103.1 ± 3.2
75 DAS	187.4 ± 3.1	166.9 ± 3.3	121.2 ± 3.1	93.1 ± 3.2

Means for age x variety

	Kharchia-65	SARC-1	PAK-81	Punjab-85
45 DAS	194.8 ± 3.2	134.5 ± 3.1	115.9 ± 3.1	109.5 ± 3.2
60 DAS	290.1 ± 3.3	186.9 ± 3.3	185.7 ± 3.1	163.5 ± 3.1
75 DAS	163.0 ± 3.1	174.0 ± 3.2	121.6 ± 3.1	110.3 ± 3.1

LSD values at $p = 0.05$

Parameters	Age	Salinity	Variety	Age x S	Age x V	S x V	A x S x V
Leaf area	19.3 ***	22.2 ***	22.2 ***	38.6 ***	38.6 *	NS	NS

All values (age x salinity x variety) are means of five observations.

except 50 mol m^{-3} NaCl. There was a significant effect of salinity on leaf area and a considerable decrease was noted in all the varieties with an increase in salt stress. At 150 mol m^{-3} stress, leaf area in Kharchia-65 was 71, 24 and 58% of the control at the first, second and third harvests respectively. In SARC-1, leaf area was decreased to 83, 25 and 57% of the control at the first, second and third harvest respectively. In PAK-81, leaf area decreased to 69, 37 and 40% of the control at the first, second and third harvest respectively. In Punjab-85, this decrease was 62, 32 and 39% of the control at first, second and third harvest respectively. Hence the trends in leaf area followed the salt resistance of the varieties. At the highest stress level, Kharchia-65, the resistant variety was able to maintain considerably higher leaf area as compared to the other varieties. SARC-1 also had higher leaf area than PAK-81 and Punjab-85 at this stress level. The lowest leaf area was recorded in the case of Punjab-85, the salt sensitive variety at 150 mol m^{-3} salinity level. At the second harvest, Kharchia-65 had the highest absolute leaf area as compared to the other varieties, while SARC-1 had the highest leaf area relative to the first harvest in control.

2.3.3 Dry Weight

Dry weight of plants at all the three harvests is presented in Table-2.2. In all the four varieties dry weight decreased considerably with increasing salinity level. At the first harvest, highest dry weight was noted in the control and at 50 mol m^{-3} NaCl in all the varieties. Kharchia-65 produced the highest dry weight as compared to the other varieties, at all the salinity levels at the first and second harvests. The effect of salt stress was not so severe at 50 mol m^{-3} NaCl, especially at the first harvest in all the four varieties. In fact there was a slight increase in dry weight at this stress level. However in the subsequent two harvests, dry weight was considerably lower at 100 and 150 mol m^{-3} NaCl stress as compared to the control. At the second harvest, dry weight of control plants of Kharchia-65 and Punjab-85 was found to be greater than that of the other two varieties. However at the two higher salinity levels, Kharchia-65 had a higher dry weight as compared to other varieties including Punjab-85. At the third harvest, dry weight of control plants of Kharchia-65, SARC-1 and Punjab-85 were almost equal and higher than that of PAK-81. At 50, 100 and 150 mol m^{-3} NaCl salinity levels however, the performance of Kharchia-65 was found to be superior to all the other tested varieties. There was a significant increase in dry matter in all the varieties due to age. The percentage increase in the third harvest over that of the first harvest in the control was the highest in SARC-1 (434 %) and Punjab-85 (427 %). At

Table - 2.2: Dry weight (g/plant) at different salinity levels (mol m^{-3} NaCl).

Varieties	Harvest	Control		50 mol m^{-3}		100 mol m^{-3}		150 mol m^{-3}	
		Means	± SE	Means	± SE	Means	± SE	Means	± SE
Kharchia-65	45 DAS	1.53	0.22	1.54	0.14	1.24	0.08	1.22	0.19
	60 DAS	3.64	0.56	3.18	0.34	1.91	0.27	1.66	0.27
	75 DAS	4.05	0.36	4.17	0.98	2.52	0.26	2.33	0.41
SARC-1	45 DAS	0.83	0.19	0.86	0.13	0.80	0.14	0.79	0.07
	60 DAS	3.04	0.61	1.39	0.34	1.15	0.22	1.05	0.26
	75 DAS	4.44	0.35	2.51	0.61	1.98	0.57	1.96	0.25
PAK-81	45 DAS	0.96	0.10	1.08	0.08	0.73	0.15	0.70	0.12
	60 DAS	2.76	0.35	2.85	0.36	1.21	0.20	1.20	0.21
	75 DAS	3.40	0.40	2.99	0.33	1.48	0.27	1.41	0.20
Punjab-85	45 DAS	0.85	0.11	1.00	0.24	0.82	0.13	0.79	0.17
	60 DAS	3.45	0.22	2.16	0.64	1.66	0.31	1.11	0.23
	75 DAS	4.48	0.68	2.93	0.46	2.08	0.36	1.29	0.15

Means for sampling dates

45 DAS	0.99 ± 0.01
60 DAS	2.09 ±0.01
75 DAS	2.76 ± 0.01

Means for salinity stress

0 mol m^{-3} NaCl	2.79 ± 0.01
50 mol m^{-3} NaCl	2.26 ± 0.01
100 mol m^{-3} NaCl	1.46 ± 0.01
150 mol m^{-3} NaCl	1.27 ± 0.01

Varietal means

Kharchia-65	2.42 ± 0.01
SARC-1	1.75 ± 0.01
PAK-81	1.73 ± 0.01
Punjab-85	1.89 ± 0.01

Means for age x salinity

	0 mol m^{-3} NaCl	50 mol m^{-3} NaCl	100 mol m^{-3} NaCl	150 mol m^{-3} NaCl
45 DAS	1.04 ± 0.03	1.12 ± 0.03	0.91 ± 0.03	0.86 ± 0.04
60 DAS	3.22 ± 0.04	2.44 ± 0.04	1.51 ± 0.04	1.19 ± 0.03
75 DAS	4.09 ± 0.04	3.22 ± 0.04	1.97 ± 0.03	1.76 ± 0.03

LSD values at p = 0.05

Parameters	Age	Salinity	Variety	Age x S	Age x V	S * V	A x S x V
Dry weight	0.24 ***	0.28 ***	0.28 ***	0.48 ***	NS	NS	NS

All values (age x salinity x variety) are means of five observations.

150 mol m^{-3} NaCl, the percentage increase in dry matter over that of the first harvest was the highest (243 %) in SARC-1 and was lowest in Punjab-85 (63 %). This shows that in the control plants the growth increment was greater in SARC-1 and Punjab-85 than in Kharchia-65. It was also evident that at 150 mol m^{-3} NaCl, depression in dry matter yield was minimum in SARC-1 and the highest in Punjab-85.

2.3.4 Length of Main Shoots and Ears

Kharchia-65 was the tallest variety at all the salinity levels tested (Table-2.3). The length of the main shoots decreased with an increase in salinity level in all the varieties. The decrease in length at 150 mol m^{-3} salinity compared to the control was 12% in Kharchia-65. The same decrease was 9, 23 and 18% in SARC-1, PAK-81 and Punjab-85 respectively.

The length of the ears also decreased with an increase in salinity (Table-2.4). Ear length was higher in Kharchia-65 than in the other varieties in all the treatments. The decrease in ear length in different varieties varied from 10 to 15% at 150 mol m^{-3} . The decrease was smaller in Kharchia-65 compared to the other varieties. Ears length was shortest in Punjab-85 at 150 mol m^{-3} salt stress.

2.3.5 Weight of Main Shoots and Ears

Weight of main shoots was recorded at the time of final harvest (Table-2.5). Weight of the main shoots was higher in Kharchia-65 as compared to the other varieties at all the tested salinity levels except those of PAK-81 at 50 and 100 mol m^{-3} NaCl. There was a considerable effect of increasing salinity on the weight of main shoots. Increasing salinity significantly decreased the weight of main shoots of all varieties. The lowest weight of shoots was noted in Punjab-85 at 150 mol m^{-3} .

Similarly, increasing salinity significantly decreased the weight of ears of all varieties except PAK-81 at 50 mol m^{-3} NaCl (Table-2.6). The weight of ears was higher in Kharchia-65 compared to the other varieties at all the stress levels except PAK-81 at 50 mol m^{-3} stress. The decrease in the weight of ears due to salt stress ranged from 34 to 54% at 150 mol m^{-3} as compared to control. The highest percentage decrease was observed in Kharchia-65, although ear weight in this variety was more than in the other varieties.

Table - 2.3: Length (cm) of main shoot in different wheat varieties at different salinity levels (mol m^{-3} NaCl) at the time of final harvest.

Varieties	**Control**		**50 mol m^{-3}**		**100 mol m^{-3}**		**150 mol m^{-3}**		Var. means
	Means	± SE	Means	± SE	Means	± SE	Means	± SE	
Kharchia-65	79.4	1.49	81.0	1.67	74.5	1.49	70.1	1.96	76.3
SARC-1	67.0	3.88	73.2	4.49	64.4	4.25	61.0	1.89	66.4
PAK-81	76.5	2.45	70.0	3.28	62.7	2.45	58.5	2.39	66.9
Punjab-85	67.3	2.3	56.6	2.03	56.1	2.71	55.2	1.62	58.8
Stress means	72.5		70.2		64.4		61.2		

LSD values at p = 0.05

Parameters	Salinity	Variety	Salinity x variety
Length of main shoot	3.58 ***	3.58 ***	NS

All values (salinity x variety) are means of ten observations.
*** = significant at $p<0.001$

Table - 2.4: Length (cm) of main ear in different wheat varieties at different salinity levels (mol m^{-3} NaCl) at the time of final harvest.

Varieties	**Control**		**50 mol m^{-3}**		**100 mol m^{-3}**		**150 mol m^{-3}**		Var. means
	Means	± SE	Means	± SE	Means	± SE	Means	± SE	
Kharchia-65	10.3	0.21	9.4	0.41	9.4	0.4	9.3	0.11	9.6
SARC-1	8.5	0.42	7.5	0.72	7.6	0.42	7.1	0.10	7.7
PAK-81	8.91	0.33	7.9	0.26	7.6	0.33	7.5	0.26	8.0
Punjab-85	8.4	0.6	7.6	0.67	7.5	0.29	7.1	0.16	7.6
Stress means	9.0		8.1		8.0		7.7		

LSD values at p = 0.05

Parameters	Salinity	Variety	Salinity x variety
Length of main ear	0.58 ***	0.58 ***	NS

All values (salinity x variety) are means of ten observations.
*** = significant at $p<0.001$

Table - 2.5: Weight (g/plant) of main shoot at final harvest in different wheat varieties at different salinity levels (mol m^{-3} NaCl).

Varieties	**Control**		**50 mol m^{-3}**		**100 mol m^{-3}**		**150 mol m^{-3}**		Var. means
	Means	± SE	Means	± SE	Means	± SE	Means	± SE	
Kharchia-65	1.39	0.2	1.42	0.14	1.09	0.11	0.89	0.06	1.20
SARC-1	0.97	0.15	1.23	0.15	0.78	0.12	0.75	0.07	0.93
PAK-81	1.19	0.15	1.53	0.14	1.10	0.23	0.83	0.07	1.16
Punjab-85	0.93	0.28	0.92	0.03	0.83	0.07	0.73	0.03	0.85
Stress means	1.12		1.28		0.95		0.80		

LSD values at p = 0.05

Parameters	Salinity	Variety	Salinity x variety
Weight of main shoot	0.20 *	0.20 ***	0.41 *

All values (salinity x variety) are means of ten observations.

*** = significant at p<0.001

* = significant at p<0.05

Table - 2.6: Weight (g/plant) of main ear at final harvest in different wheat varieties at different salinity levels (mol m^{-3} NaCl).

Varieties	**Control**		**50 mol m^{-3}**		**100 mol m^{-3}**		**150 mol m^{-3}**		Var. means
	Means	± SE	Means	± SE	Means	± SE	Means	± SE	
Kharchia-65	1.70	0.18	1.21	0.08	1.10	0.05	0.78	0.07	1.20
SARC-1	1.19	0.15	1.16	0.14	0.98	0.12	0.72	0.10	1.01
PAK-81	1.02	0.12	1.37	0.12	0.99	0.08	0.61	0.09	1.00
Punjab-85	1.07	0.13	0.88	0.14	0.79	0.11	0.71	0.10	0.86
Stress means	1.24		1.16		0.97		0.71		

LSD values at p = 0.05

Parameters	Salinity	Variety	Salinity x variety
Weight of ear	0.14 ***	0.14 ***	0.28 *

All values (salinity x variety) are means of ten observations.

*** = significant at p<0.001

* = significant at p<0.05

2.3.6 Total Number of Tillers and Ears

Total number of tillers and ears per plant was recorded at the time of final harvest and is presented in Tables - 2.7 & 2.8 respectively. There was a significant decrease in these parameters with an increase in the salinity level. However, in SARC-1, there was no decrease in the number of ears per plant at 50 mol m^{-3} NaCl. Highest total numbers of tillers per plant were recorded in Kharchia-65 as compared to all the other varieties at all the salinity levels. The number of ears was also the highest in this variety in the control, at 100 mol m^{-3} and 150 mol m^{-3} NaCl while at 50 mol m^{-3} NaCl, number of ears was highest in SARC-1. The lowest number of total tillers were found in PAK-81 at all the stress levels. The number of ears were the lowest in PAK-81 and Punjab-85 at control, 50 mol m^{-3} and 100 mol m^{-3} NaCl. However, at 150 mol m^{-3} NaCl, number of ears were almost equal in SARC-1, PAK-81 and the salt-sensitive variety Punjab-85 and were the highest in the salt-tolerant variety Kharchia-65.

2.3.7 Relative Growth Rate

Relative growth rate (RGR) decreased with an increase in the salinity level in all the varieties except Kharchia-65 where a slight increase was noted at 50 mol m^{-3} NaCl (Table-2.9). In the control, 50 mol m^{-3} and 100 mol m^{-3} NaCl, the highest growth rates were found in SARC-1 and Punjab-85. At the highest salinity level of 150 mol m^{-3} NaCl however, SARC-1 had a significantly higher relative growth rate as compared to all the other varieties while in Punjab-85, it was the lowest. Effect of salinity was significant while those of variety and salinity x variety was found to be non-significant.

2.3.8 Grain Yield per Main Shoot Ear

Number of grains, weight of grains and 100 grain weight of the main shoot ears of different wheat varieties at different salinity levels are shown in Table-2.10. Number of grains, total grain weight per plant and 100 grain weight were generally found to decrease significantly with an increase in salinity levels. In control plants, the highest number and weight of grains was recorded in Kharchia-65, which decreased with an increase in salinity level. At 150 mol m^{-3} salinity level, grain weight in this variety was only 0.45g. In SARC-1 and PAK-81 grain weight was generally maximum at 50 mol m^{-3} and then decreased at higher salinity levels. At 150 mol m^{-3}, grain weight was highest in SARC-1 which was slightly higher than that of Kharchia-65. In control plants 100 grain weight was highest in Kharchia-65 and the lowest in Punjab-85. In all the

Table - 2.7: Number of total tillers per plant at final harvest in different wheat varieties at different salinity levels (mol m^{-3} NaCl).

Varieties	Control		50 mol m^{-3}		100 mol m^{-3}		150 mol m^{-3}		Var. means
	Means	± SE	Means	± SE	Means	± SE	Means	± SE	
Kharchia-65	5.6	0.7	4.7	0.2	3.2	0.1	2.5	0.2	4.0
SARC-1	4.4	1.2	4.4	0.9	2.7	0.5	2.2	0.3	3.4
PAK-81	2.8	0.3	1.8	0.3	1.2	0.1	1.2	0.1	1.8
Punjab-85	3.3	0.7	2.3	0.2	2.0	0.3	2.0	0.2	2.4
Stress means	4.0		3.3		2.3		1.98		

LSD values at p = 0.05

Parameters	Salinity	Variety	Salinity x variety
Total tillers/plant	0.73 ***	0.73 ***	NS

All values (salinity x variety) are means of ten observations.
*** = significant at $p<0.001$

Table - 2.8: Number of ears per plant at final harvest in different wheat varieties at different salinity levels (mol m^{-3} NaCl).

Varieties	Control		50 mol m^{-3}		100 mol m^{-3}		150 mol m^{-3}		Var. means
	Means	± SE	Means	± SE	Means	± SE	Means	± SE	
Kharchia-65	3.8	0.8	3.0	0.4	1.8	0.3	1.8	0.2	2.6
SARC-1	2.8	0.8	3.7	0.7	1.6	0.4	1.5	0.1	2.4
PAK-81	2.1	0.3	1.5	0.2	1.1	0.1	1.1	0.1	1.5
Punjab-85	2.4	0.4	1.2	0.1	1.4	0.2	1.2	0.1	1.6
Stress means	2.8		2.4		1.5		1.4		

LSD values at p = 0.05

Parameters	Salinity	Variety	Salinity x variety
Ears/plant	0.60 ***	0.60 ***	NS

All values (salinity x variety) are means of ten observations.
*** = significant at $p<0.001$

Table - 2.9: Relative growth rate per plant (mg per g per day) of different wheat varieties at different salinity levels (at 75 DAS over 45 DAS).

Varieties	**Control**		**50 mol m^{-3}**		**100 mol m^{-3}**		**150 mol m^{-3}**		Var. means
	Means	± SE	Means	± SE	Means	± SE	Means	± SE	
Kharchia-65	33.3	4.87	33.2	1.88	23.6	4.26	21.6	3.30	27.9
SARC-1	58.6	6.97	35.7	4.37	30.2	5.30	30.3	4.44	38.7
PAK-81	43.4	9.48	33.9	5.33	23.6	6.32	23.3	6.84	31.1
Punjab-85	54.6	5.09	35.7	9.62	31.0	6.10	16.3	5.97	34.4
Stress means	47.5		34.6		27.1		22.9		

All values (salinity x variety) are means of five observations.

LSD values at p = 0.05

Parameters	Salinity	Variety	Salinity x variety
Relative growth rate	9.99 ***	NS	NS

*** = significant at p<0.001

Table - 2.10: Effect of salinity (mol m^{-3} NaCl) on grain weight/spike and yield components of different wheat varieties.

Varieties	Parameters	Control		50 mol m^{-3}		100 mol m^{-3}		150 mol m^{-3}	
		Means	±SE	Means	±SE	Means	±SE	Means	±SE
Kharchia-65	No. of grains/ear	43.50	3.40	31.25	2.71	29.40	2.63	27.80	2.33
	Wt. of grains(g)/ear	1.30	0.15	1.01	0.06	0.66	0.03	0.45	0.04
	100 Gr. wt. (g)	2.92	0.19	3.37	0.24	2.38	0.21	1.60	0.10
SARC-1	No. of grains/ear	24.90	2.52	21.10	2.68	20.56	2.10	20.00	1.13
	Wt. of grains(g)/ear	0.82	0.12	0.91	0.13	0.64	0.07	0.49	0.09
	100 Gr. wt. (g)	3.28	0.52	4.23	0.15	3.17	0.22	2.54	0.33
PAK-81	No. of grains/ear	28.40	2.86	37.30	3.26	29.00	2.83	22.50	4.33
	Wt. of grains(g)/ear	0.81	0.10	1.06	0.11	0.69	0.05	0.38	0.08
	100 Gr. wt. (g)	2.84	0.20	2.88	0.26	2.42	0.21	1.73	0.24
Punjab-85	No. of grains/ear	29.30	2.59	26.70	3.84	24.60	2.90	21.70	2.08
	Wt. of grains(g)/ear	0.75	0.08	0.62	0.10	0.56	0.08	0.32	0.09
	100 Gr. wt. (g)	2.54	0.17	2.35	0.28	2.28	0.21	1.52	0.19

Means for salinity stress

	0 mol m^{-3} NaCl	50 mol m^{-3} NaCl	100 mol m^{-3}NaCl	150 mol m^{-3} NaCl
No. of grains/ear	31.5	29.2	25.89	23.0
Wt. of grains/ear	0.93	0.91	0.62	0.40
100 Gr. wt (g)	2.90	3.22	2.56	1.84

Varietal means

	Kharchia-65	SARC-1	PAK-81	Punjab-85
No. of grains/ear	33.0	21.5	29.5	25.6
Wt. of grains/ear	0.85	0.72	0.74	0.56
100 Gr. wt (g)	2.57	3.28	2.45	2.17

LSD values at $p = 0.05$

Parameters	Salinity	Variety	Salinity x variety
Number of grains/main ear	3.30 ***	3.30 ***	6.67 *
Weight of grains/ main ear	0.12 ***	0.12 ***	0.25 *
100 grain weight	0.33 ***	0.33 ***	NS

All values (salinity x variety) are means of ten observations.

*** = significant at $p<0.001$, * = significant at $p<0.05$

varieties except Punjab-85, the highest 100 grain weight was recorded at 50 mol m^{-3} NaCl, the highest value being recorded in SARC-1. At 150 mol m^{-3} stress, 100 grain weight of SARC-1 and PAK-81 was higher than in Kharchia-65 and Punjab-85. The lowest number of grains, grain weight and 100 grain weight was recorded in the salt-sensitive variety Punjab-85.

Variety x salinity interaction was significant for number and weight of grains per main stem ear which indicated that performance of varieties for these parameters was significantly different at different salinity levels.

2.4 Correlation of Results

To study the inter-relationships between yield, yield components, and growth characteristics, linear correlation coefficients were calculated for each variety. As highest leaf area was recorded at the second harvest, leaf area and dry weight at this stage were correlated with values of yield and yield components at maturity, to determine if the effects of salinity on growth at this stage were correlated with the effects at maturity.

As salt stress decreased growth, there was negative correlation of some parameters with the amount of added NaCl stress (0=control, 50 mol m^{-3} NaCl, 100 mol m^{-3} NaCl, 150 mol m^{-3} NaCl) in all the varieties (Table-2.11). In Kharchia-65, there was a highly significant negative correlation between stress and leaf area, dry weight, weight of grains and total number of tillers. The values of the linear correlation coefficients between number of grains, 100 grain weight, number of ears per plant and stress were also quite high ($r = 0.88$) but were non-significant. The correlations of leaf area with dry weight, weight of grains per plant and total number of tillers were also significant and were high ($r = 0.85$) but with number of grains per plant, 100 grain weight and number of ears per plant were non-significant. Dry weight at the second harvest was also significantly correlated with the weight of grains per plant, total number of tillers and ears per plant. In SARC-1, there was a highly significant negative correlation between stress and leaf area recorded at the second harvest. Leaf area and dry weight per plant at the second harvest were also significantly correlated with the number of grains per plant. All the other correlations were non-significant.

In PAK-81, there were negative but non-significant correlations between stress and other growth parameters which were quite high in the case of leaf area, dry weight, weight of grains, 100 grain weight, total number of tillers and ears. Significant positive correlation was only noted in between leaf area an dry weight. All other correlations between leaf area and dry weight with

Table - 2.11: Values of the linear correlation coefficient between salinity levels (mol m^{-3} NaCl), leaf area and dry weight at second harvest and total number of tillers, number of ears, number of grains, weight of grains and 100 grain weight.

Varieties	Parameters	Leaf Area	Dry Wt.	NOG	WOG	100 Gwt	TTill	Ears
Kharchia-65								
	Salinity	-0.998 **	-0.967 *	-0.884 NS	-0.995 **	-0.903 NS	-0.991 **	-0.949 NS
	Leaf area		0.972 *	0.858 NS	0.991 **	0.924 NS	0.992 **	0.945 NS
	Dry weight			0.837 NS	0.974 *	0.884 NS	0.993 **	0.984 *
SARC-1								
	Salinity	-0.971 *	-0.860NS	-0.887 NS	-0.868 NS	-0.634 NS	-0.936 NS	-0.791 NS
	Leaf area		0.953 *	0.966 *	0.747 NS	0.454 NS	0.871 NS	0.674 NS
	Dry weight			0.998 **	0.511 NS	0.164 NS	0.687 NS	0.426 NS
PAK-81								
	Salinity	-0.941 NS	-0.883NS	-0.508 NS	-0.759 NS	-0.929 NS	-0.899 NS	-0.929 NS
	Leaf area		0.981 *	0.499 NS	0.767 NS	0.885 NS	0.901 NS	0.923 NS
	Dry weight			0.605 NS	0.833 NS	0.888 NS	0.805 NS	0.834 NS
Punjab-85								
	Salinity	-0.908 NS	-0.971 *	-0.995 **	-0.968 *	-0.896 NS	-0.562 NS	-0.764 NS
	Leaf area		0.978 *	0.882 NS	0.821 NS	0.680 NS	0.827 NS	0.933 NS
	Dry weight			0.959 *	0.921 NS	0.817 NS	0.742 NS	0.893 NS
All Variet ies(Pooled)								
	Salinity	*-0.844****	*-0.853****	*-0.519 **	*-0.793****	*-0.642***	*-0.607***	*-0.671***
	Leaf area		*0.920****	*0.699***	*0.859****	*0.518**	*0.815****	*0.801****
	Dry weight			*0.726****	*0.753****	*0.330 NS*	*0.618 ***	*0.609***

Degree of freedom for individual varieties = 2, and for pooled data = 14

Ttill = Total number of tillers per plant.

Ears = Total number of ears per plant.

* = Significant at 5% level of significance.

** = Significant at 1% level of significance.

NS = Non-significant at 5 and 1% level of significance.

NOG = Number of grains per main ear. WOG = Weight of grains per main ear.

100 Gwt = 100 grain weight.

yield parameters and number of total tillers and ears were non-significant.

In Punjab-85, significant negative correlations were found between stress and dry weight, number and weight of grains per plant. There was a significant positive correlation between leaf area and dry weight. Dry weight per plant and number of grains per plant were also significantly correlated (r = 0.959). All other correlations were quite high but non-significant.

Coefficients of linear correlation were also computed between different parameters on the pooled data of all the varieties (Table - 2.11). A significant and positive correlation was found between leaf area and dry weight with the number and weight of grains per ear, number of total ears per plant and number of ears per plant. Hundred grain weight was however correlated significantly only with leaf area and not with the dry weight of main shoots. There was a significant but negative correlation (r = -0.519 to -0.844) of increasing salinity levels with all the above mentioned yield and growth parameters.

2.5 DISCUSSION

The four wheat varieties included in this study have been shown to differ in their salt tolerance (Storey and Wyn-Jones, 1978; Qureshi *et al.* 1980; Kingsbury and Epstein, 1984; Rawson *et al.* 1988; Ashraf and McNeilly, 1991 and Qureshi *et al.* 1993).

The data obtained in this study suggest that SARC-1 and Kharchia-65 had superior salt tolerance to the other two varieties. SARC-1 gave higher grain weight at 150 mol m^{-3} salinity than the other salt-tolerant variety Kharchia-65. Although the absolute grain weight of Kharchia-65 was almost equal to that of SARC-1 (Table - 2.10), the percentage decreases in number of grains, weight of grains per ear and 100 grain weight at 150 mol m^{-3} NaCl were greater in Kharchia-65 compared to all the other varieties. There were also significant negative correlations between salinity and leaf area, dry weight and weight of grains per ear in Kharchia-65 (Table - 2.11), but in SARC-1, these correlations were significant only for leaf area (r = -0.971). The comparatively better performance of SARC-1 might be due to its ability to maintain a higher level of leaf area at the later growth stages, a higher RGR at increased salinity levels and comparatively better grain development as is evident from its higher 100 grain weight. Both these varieties also had higher number of ears per plant. As a result of the ability of these varieties i.e. SARC-1 and Kharchia-65, to maintain higher leaf area and ear size under salt stress, grain weight was comparatively greater than in the other tested varieties. Srivastava *et al.* (1988) also attributed the better performance of Kharchia-65 to its potential for maintaining higher photosynthetic area and higher photosynthetic efficiency under saline conditions.

Number of grains, weight of grains and 100 grain weight were decreased significantly by salinity stress. At 150 mol m^{-3} , weight of grains and 100 grain weight were the lowest in the salt-sensitive variety Punjab-85. At the same salinity level, highest weight of grains and 100 grain weight was noted in SARC-1.

At low salt stress (50 mol m^{-3} NaCl) there was a slight increase in the weight of grains in SARC-1 and PAK-81. Leidi and Lips (1990) and Salama *et al.* (1994) observed the same phenomenon at 50 mol m^{-3} salinity in wheat and attributed it to enhanced translocation of assimilates induced by salinity. In this study however, this mechanism was not visible in Kharchia-65 and Punjab-85.

Decreases in the grain weight due to salinity were greatest in the salt-sensitive varieties Punjab-85 and PAK-81 and were due mainly to decreases in the leaf area, dry weight and weight of ears. Ashraf and McNeilly (1991) have also reported that Punjab-85 is sensitive to salt stress. At 150 mol m^{-3} salinity level, Punjab-85 had higher number of grains than SARC-1 but its grain weight was very low suggesting the presence of some inhibitory mechanism which hindered the translocation of assimilates to the grains resulting in low grain yield per ear and lowest 100 grain weight.

There were varietal difference in the changing patterns of relative growth rate (RGR) to NaCl salinity of the culture medium. In the absence of salinity, RGR was greatest in SARC-1 and Punjab-85 but it decreased with increasing levels of salinity (Table - 2.9). At 150 mol m^{-3} salinity, RGR in Punjab-85 decreased considerably and was the lowest of all the tested varieties but it was still the highest in SARC-1. This indicates that Punjab-85 was quite a productive variety in the absence of salt stress but is not suitable for salt stressed soil conditions due to its salt-sensitive nature. The results are similar to those of Kuiper *et al.* (1990) who reported that after about 14 days, NaCl salinity (65 mol NaCl m^{-3}) induced severe decreases in RGR values in wheat and barley.

Other agronomic characters such as length of main shoot and ears, weight of main shoots and ears, number of total tillers and ears per plant were also significantly decreased due to increasing salinity levels especially at 100 and 150 mol m^{-3} NaCl salinity and there were significant differences in between the varieties in all these parameters. Kharchia-65 was the tallest variety even at 150 mol m^{-3} salinity, had higher average weight per main shoot and ear and average number of the total tillers and ears and as a result it produced higher grain weight as compared to the salt-sensitive varieties Punjab-85 and PAK-81. Francois *et al.* (1994) reported a decrease in tiller number, number of ears, grain number and weight of grains in wheat as a result of increased salinity.

A significant decrease was noted at higher salinity levels in all the measured parameters in all the four varieties. At 50 mol m^{-3} however, there was a slight increase in length and dry weight of the main tillers and ears in some varieties. Leaf area was significantly increased at 60 DAS as compared to 45 DAS and then decreased significantly at 75 DAS as compared to 60 DAS (Table - 2.1). Averaged over the three harvesting dates and stress levels, leaf area was the highest in Kharchia-65 and SARC-1 as compared to the two other varieties. Similarly, averaged for the four varieties and stress levels, highest leaf area was noted at 60 DAS during the period of peak vegetative growth. The decrease in leaf area at 75 DAS was induced by senescence due to salt accumulation in the leaves and ageing (Munns and Termaat, 1986). Lowest leaf area was noted in Punjab-85 at 150 mol m^{-3} salinity as compared to other varieties at 75 DAS. Averaged over sampling dates and varieties, salinity at 100 and 150 mol m^{-3} NaCl caused a significant decrease in leaf area. Decrease in leaf growth under salinity stress may be due to a decrease in leaf turgor (Neumann *et al.* 1988) or due to reduced N, P and K^+ uptake by the plants due to NaCl stress (Dale, 1982). Decrease in leaf area and other agronomic characteristics (shoot and root weight) at increased salinity level was also reported by Mahmood and Quarrie (1993).

There was a considerable reduction in dry matter accumulation in all the varieties with increasing levels of salt stress (Table - 2.2). This effect was also reported by other researchers (Pessarakli *et al.* 1991; Kalaji and Nalborczyk, 1991). Maximum effect of salt stress was noted in case of Punjab-85 in which leaf area was adversely affected which resulted in less grains and dry matter. Salt sensitivity of Punjab-85 was also reported by Ashraf and McNeilly (1991) while comparing it with LU26S.

2.6 CONCLUSIONS

Different wheat varieties responded differently to salt stress. SARC-1 and Kharchia-65 showed better performance than the salt-sensitive variety Punjab-85 and PAK-81. Kharchia-65 and SARC-1 were able to maintain higher leaf area, dry weight and RGR than other varieties at elevated salt stress which might be a reason for their better yield and superior salt tolerance. At 150 mol m^{-3} NaCl stress, hundred grain weight in Kharchia-65 was lower than SARC-1 and PAK-81 in spite of the fact that its leaf area and dry weight was the highest. This suggests the presence of some inhibitory mechanism which hindered the translocation of assimilates from the leaves to the seeds at high salinity.

Punjab-85 proved to be a suitable variety under non-saline conditions but its yield (WOG) and 100 grain weight under higher salinity levels was very low which rendered this variety to be sensitive to salt stress and unsuitable for salt affected soils.

CHAPTER 3

PERFORMANCE OF WHEAT VARIETIES DIFFERING IN SALT TOLERANCE UNDER SALINE FIELD CONDITIONS IN PAKISTAN

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3.1 INTRODUCTION

Salt tolerance studies are often carried out in solution culture under controlled environment or glasshouse conditions because it is possible to maintain uniform salinity levels in the culture medium. These conditions are usually best suited for optimum crop growth. Solution culture techniques though good for physiological studies on plants, do not provide a realistic prediction of how the plants will behave in the field. Plant roots may face more heterogeneous conditions in fields as compared with solution culture (Rashid, 1990). There are numerous ways in which soil salinity, soil fertility, water supply and weather conditions in the field can be substantially different from the conditions maintained in a growth room or glasshouse in solution culture. There is every likelihood that differences in these growth conditions might alter the response of crop cultivars to salt stress. In a glasshouse the seedlings are often pre-germinated in salt free media (e.g. in sand or on capillary matting), to obtain a uniform stand in the experiment; whereas under field conditions the seeds are sown directly into the saline/sodic soil and the seedlings have to undergo salt stress immediately after their germination. It has been reported that most crop plants attain increased salt tolerance at later growth stages (Maas, 1984). Hence this may also contribute to variable responses between systems. In the field also, the responses of cultivars may be quite different under different types of salt stresses. Keeping this in mind, two experiments were performed under saline and sodic field conditions on different wheat varieties.

A predominant type of salt stress is found in 'saline soils'. These soils contain low exchangeable sodium but contain excessive concentrations of soluble salts and the electrical conductivity of the saturation extract (EC_e) from these soils is always more than 4 dS m^{-1}. Excessive amounts of soluble salts produce harmful effects by increasing the salt content of the soil solution. The exchangeable sodium percentage of the soil is always less than 15 and the pH of the soil is always less than 8.5. The crop plants suffer in these soils mostly due to osmotic effects (Richards, 1969). Accumulation of excessive Na^+ causes premature senescence of leaves, and hence the ability of the plants to limit the accumulation of Na^+ in leaves can serve as an important mechanism in salt tolerance (Schachtman and Munns, 1992). Kingsbury and Epstein (1986) found that the salt composition of different isosmotic solutions had little effect on the growth of a salt tolerant wheat line but a sensitive line was affected significantly. The sensitive line tended to accumulate more Na^+ than the tolerant line under high Na^+ concentration of the growth medium. They suggested that superior compartmentation of toxic ions, principally Na^+, may be a mechanism of salt tolerance.

This first experiment was conducted under field conditions on a saline soil to compare and study the yield potential of different wheat varieties, to study sodium and potassium concentrations in the flag leaves and to correlate these with the yield and yield components of the different varieties.

3.2 MATERIALS AND METHODS

3.2.1 Experimental Materials

3.2.1.1 Wheat Seeds

The following six wheat varieties were selected for comparison in this experiment. All these varieties were also included in the experiment conducted on a dense sodic soil (Chapter 5). The seeds were collected from Soil Science Department (Saline Agriculture Programme), of the University of Agriculture, Faisalabad, Pakistan.

1. SARC-1	Moderately tolerant to tolerant
2. SARC-2	Moderately tolerant
3. SARC-3	Moderately tolerant
4. SARC-4	Moderately tolerant
5. LU26S	Salt tolerant
6. Punjab-85	Salt sensitive

3.2.1.2 The Soil and Soil Preparation

The experiment was conducted at the Soil Salinity Research Institute, Pindi Bhattian, Pakistan; where the soil was well-drained and the water table remained below 3 metres during most of the year (Table-3.1). The experiment was carried out at two adjacent sites which were about 300 metres apart. One site was a 'normal' soil which had been previously reclaimed with excessive leaching with good quality water and had been under cropping for the last 7 years (EC_e < 4.0 dS m^{-1}; pH < 8.5 and ESP < 15.0). The soil was classed as a non-saline soil according to the criteria of the United States Department of Agriculture (Richards, 1969). The other site was a 'saline' soil (EC_e > 4.0 dS m^{-1}, pH < 8.5 and ESP < 15.0). The texture of the soil at both the sites was sandy loam. The crop rotation followed at the farm was wheat-rice-wheat. Soil analysis was conducted to assess the nature and magnitude of the stress. Soil salinity was monitored at different growth stages of the wheat. Site preparation began in October with a heavy irrigation with good quality irrigation water to leach down the excessive salts. When the soil was in a proper moisture condition a fine seed bed was prepared. Soil samples were collected from fifteen different locations at random from each site before fertilizer application and sowing. A composite sample (1 kg) was made out of these for analysis in the laboratory. The second soil sampling was made at the time of booting and the final sampling was done at the time of harvest. These samples were analyzed using the analytical procedures described by Richards (1969). The following parameters were determined.

- Electrical conductivity of the saturation paste extract (EC_e) in dS m^{-1}. The paste was prepared in distilled water.
- The pH (saturation paste in distilled water) was measured with a conductivity meter (Beckman, USA).
- Soluble carbonates (CO_3^{2-}) and bicarbonates (HCO_3^-) were determined by titration against standard sulphuric acid. Chlorides (Cl^-) were estimated by titration with $AgNO_3$ solution. Ca^{2+}+Mg^{2+} was determined by titration with Ethylenediaminetetraacetate (Versenate) solution from a specially prepared soil extract. Sodium was estimated by flame photometer (Beckman, USA) using the saturation paste extract.
- Exchangeable Na^+ percentage (ESP) was determined directly as well as conversion from SAR. SAR was calculated using soluble Na^+ and Ca^{2+}+Mg^{2+} concentrations. Conversion of SAR to ESP was done using the following regression equation (Richards, 1969).

ESP= {100 (-0.126+0.01475 x)}/{1+(-0.01475 x)} where 'x' is equal to SAR.

After the first soil sampling, fertilizer was applied according to the recommended rates for wheat in that area i.e. 135 kg N ha^{-1}, 110 kg P_2O_5 ha^{-1} and 60 kg K_2O ha^{-1}, as urea, single superphosphate and potassium sulphate respectively. One third of the nitrogen and all the phosphorus and potassium were applied before sowing. The remaining nitrogen was applied in two equal splits with the first and third irrigation. This split nitrogen application was done to minimise any losses through leaching due to the coarse texture of this soil.

The EC_e of the normal soil further decreased during the period of wheat growth due to leaching of the salts to lower horizons (Table 3.1). At the time of harvest, it had dropped to 0.8 dS m^{-1}. There was also a small decrease in pH and larger decreases in chlorides, Ca^{2+}+Mg^{2+}, Na^{+}, SAR and ESP of the soil by the time of harvest.

The other soil was a saline soil with medium salinity. The soil had some spatial variability at this site and the data for soil analysis reported in Table-3.1 is from a soil sample composited from 15 soil samples collected randomly from different parts of the field. Igartua (1995) also reported a high spatial variability in salt affected fields. At the start of the experiment, its EC_e was about 6 times higher than the normal soil. A decrease in EC_e was noted at booting but at the time of final harvest, it was even greater than at sowing. pH was close to 8.5 throughout the duration of the experiment. Cl^{-}, Ca^{2+}, Mg^{2+}, Na^{+}, SAR and ESP were all considerably higher than in the normal soil. During the growth period there were considerable decreases in HCO_3^{2-}, Cl^{-} and Ca^{2+}+Mg^{2+}. Soluble Na^{+} was lower at booting than at sowing but became higher at the time of final harvest. SAR and ESP increased during the growth period. The data showed that at all the three growth stages, the soil remained a saline soil ($EC_e > 4.0$, pH < 8.5 and ESP > 15.0) in spite of the increases in soluble sodium.

3.2.1.3 Sowing

The experiment was sown on November 28, 1993 according to a randomized complete block design. Sowing was done with a single row cotton drill keeping the row to row distance at 30 cm. There were three replications at each site. Each block was partitioned into 6 plots. Each plot was assigned to one variety and was 10 m long and consisted of 7 rows.

Table - 3.1: Physico-chemical soil characteristics (electrical conductivity of saturation paste extract in dS m^{-1}(ECe), pH of saturation paste, soluble carbonates (CO_3^{2-}), bicarbonates (HCO_3^-), chlorides (Cl^-), calcium plus magnesium (Ca^{2+}+Mg^{2+}) sodium (Na^+), sodium adsorption ratio (SAR) and exchangeable sodium percentage (ESP).

Time of sampling	ECe dS m^{-1}	pH	CO_3^{2-}	HCO_3^-	Cl^-	Ca^{2+}+Mg^{2+}	Na^+	SAR	ESP *
Normal soil	(0-15cm)								
Sowing	1.9	8.4	-	5.7	8.8	6.1	10.0	5.7	6.7 (6.1) *
Booting	1.5	8.3	-	2.7	4.7	3.9	7.8	5.6	6.5 (5.9)
Harvest	0.8	8.3	-	3.0	1.4	4.4	4.4	3.0	3.0 (3.6)
Saline soil	(0-15cm)								
Sowing	12.7	8.6	Traces	9.5	97.7	15.1	110.3	40.1	36.7 (14.7)
Booting	9.7	8.5	-	3.3	77.1	8.2	87.2	43.0	38.4 (14.5)
Harvest	15.8	8.3	-	5.2	45.6	9.1	119.0	55.8	44.8 (14.9)

* ESP values within the parentheses are actual values obtained through laboratory assay of exchangeable Na^+. ESP values outside the parentheses were calculated from SAR data.

* Concentration of CO_3^{2-}, HCO_3^-, Cl^-, Ca^{2+} + Mg^{2+} and Na^+ are in meq. per litre (me l^{-1}).

3.2.2 Maintenance of the Experiment

After the germination of the crop, thinning was done and a plant to plant distance of approximately 2.5 cm was established. Irrigation was applied according to the crop demand with a 1:1 mixture of good quality canal water and tube well water of marginal quality. At each irrigation the plots were flooded to a depth of approximately 8 cm. A total of 5 irrigations were applied up to the maturity of the crop. Manual hoeing was carried out after the first and second irrigations to eradicate the weeds which were abundantly growing in the non-saline soil but less so in the saline soil.

3.2.3 Visual Observations

Germination and emergence of all the varieties was patchy in the saline soil and was more uniform in normal soil. In the normal soil, growth of all the varieties seemed to be equal while in the saline soil, growth of Punjab-85 was quite stunted as compared to the other varieties. There was no noticeable insect or disease attack in the normal as well as the saline soil throughout the growth period.

3.2.4 Growth Measurements

The following data were recorded.

1. Flag leaf area was determined at the time of anthesis on March 26, 1994 using the following formula as mentioned in Chapter 2 (section 2.2.6):

   Leaf area = (0.9 x Length)*(0.5 x Width) .... (Robson and Sheehy, 1980).

   Five flag leaves were taken at random from each plot to determine the leaf area.

2. Thirty flag leaves (10 from each replication) were collected from each treatment and variety. These were stored in labelled paper bags and were dried in an oven at 70 °C for 72 hours and weighed.

The soluble ions from the leaves were extracted in 20 ml pyrex test tubes in 10 ml of 0.1 M acetic acid at 80°C in a water bath for 1.5 hours. The whole leaf was kept submerged in the acetic acid to ensure full extraction. The open ends of the test tubes were covered tightly with cling film to avoid any evaporation and changes in concentration of the extracted ions.

The concentrations of sodium and potassium in this extract were measured by atomic absorption spectrophotometer (Pye Unicam Model SP-919) at the School of Biological Sciences, University of Sussex, Brighton.

3. Thirty plants (10 from each replication) were harvested at maturity from each treatment and variety. The following data were recorded:

i. No. of tillers per plant
ii. No. of ears per plant
iii. Length of main shoots and spikes
iv. Total weight of main shoots and spikes
v. Number of grains in spikes from main shoots
vi. Weight of grains per main spike
vii. 100 grain weight

3.2.5 Statistical Analysis

The data for the two sites were combined and analyzed using analysis of variance according to the procedure for experiments repeated over different sites described by Cochran & Cox (1957) using Minitab statistical package for Windows v. 10.2. An example of the anova table is presented in Appendix - 3.1. Where treatment effects were significant, differences between means were tested by LSD values which were calculated by the equation described in Chapter 2 (section 2.2.8). Significance levels are presented in the tables by * , **, *** for 5%, 1% and 0.1 probability levels, respectively. Non-significant effects are shown as 'NS'. All LSD values among means in the text were calculated at the 0.05 level of probability unless otherwise stated.

As there were large differences between Na^+ contents and K^+/Na^+ ratios of flag leaves of plants grown in the normal (non-saline) and saline soil, separate statistical analysis were done for each for these two parameters and LSDs were calculated accordingly.

3.3 RESULTS

3.3.1 Flag Leaf Area

Data for flag leaf area (cm^2) at anthesis stage are presented in Table - 3.2. The effects of salinity were highly significant ($P < 0.01$) while those of variety and the variety x salinity interaction were non-significant. In the saline soil there was a highly significant decrease in flag leaf area which ranged from 50% in salt-sensitive variety Punjab-85 to 63% in SARC-4. Decrease in leaf area in salt-tolerant variety LU26S was about 56% .

3.3.2 Length of Main Shoots and Spikes

Length of main shoots and spikes in different varieties is presented in Table-3.3. The effects of salinity and variety on main shoot length and the variety x salinity interaction were significant. In this experiment, SARC-2 was the tallest variety in normal soil but its stem length was not significantly different from that of all other varieties except SARC-1 and Punjab-85 which was the shortest. There was a significant decrease in the length of main shoots in saline soil which ranged from 24% in the moderately salt tolerant variety SARC-2 to 44% in the salt sensitive variety Punjab-85. The effects of salinity on length of main shoots were least in the moderately salt tolerant variety SARC-1 (24%) followed by salt tolerant variety LU26S (26%).

For spike length, the effects of variety and salinity were found to be significant while their interaction was non-significant. Spike length in normal soil was highest in SARC-3, which was statistically similar to all other varieties except Punjab-85, which had the shortest spikes. There was a considerable decrease in spike length of these varieties due to salt stress which ranged from 8% in SARC-1 to 28% in SARC-3. In the saline soil, spike length was lowest in the salt sensitive variety Punjab-85. The longest spikes were noted in SARC-2 followed by LU26S. In LU26S and SARC-2 the lengths of spikes recorded in saline soil were similar to those found in normal soil.

3.3.3 Weight of Main Shoots and Spikes

A very large reduction in the weight of main shoots was noted in all the varieties under saline conditions. It ranged from 21% in SARC-2 to 56% in Punjab-85 (Table - 3.4), although the variety x salinity interaction was not significant. The variety x salinity interaction was non-significant, which showed that the varieties performed similarly at the two sites. Averaged over the two sites, main shoot weight was highest in SARC-2 and LU26S but these varieties were similar to SARC-3 and SARC-4. Lowest main shoot weight was noted in Punjab-85.

Table - 3.2: Flag leaf area (cm^2) of different wheat varieties.

Varieties	**Normal soil**		**Saline soil**	
	Means	±SE	Means	±SE
SARC-1	19.4	2.00	8.9	1.30
SARC-2	21.0	1.40	10.4	1.48
SARC-3	20.1	1.49	8.7	0.42
SARC-4	21.8	2.40	8.2	1.50
LU26S	18.8	0.99	8.3	0.65
Punjab-85	19.2	1.03	9.6	1.40
Site means	20.0		9.0	

LSD values at p = 0.05
Site means = 1.74 (***); Variety means = (NS); V x S means = (NS)
All values are means of fifteen observations.

Table - 3.3: Length (cm) of main shoots and spikes.

Varieties	**Normal soil**				**Saline soil**				Variety means	
	Main shoots		Spikes		Main shoots		Spikes		Shoots	Spikes
	Means	± SE	Means	± SE	Means	± SE	Means	±SE		
SARC-1	84	2.2	9.2	0.2	64	1.4	8.5	0.7	74	8.9
SARC-2	104	2.8	10.4	0.4	79	1.0	9.6	0.2	92	10.0
SARC-3	101	6.6	10.7	0.2	58	7.2	7.7	0.6	80	9.2
SARC-4	98	2.4	9.6	0.3	69	5.9	8.5	0.7	84	9.0
LU26S	100	2.4	10.2	0.3	74	0.7	9.4	0.3	87	9.8
Punjab-85	92	0.5	9.0	0.1	51	4.5	7.2	0.2	72	8.1
Site means	97		9.9		66		8.5			

LSD values at p = 0.05
Site means for length of main shoots = 4.66 (***), length of spikes = 0.49 (***)
Variety means for length of main shoots = 7.94 (***), length of spikes = 0.84 (**)
V x S means for length of main shoots = 11.23 (*), length of spikes = (NS)
All values are means of thirty observations.

Weight of main shoot spikes was also decreased considerably in saline soil as compared to the normal soil. The decrease ranged from 13% in SARC-2 to 52% in SARC-3 (Table -3.4), although the variety x salinity interaction was not significant. Averaged over the two sites, weight of spikes was significantly higher in the salt tolerant variety LU26S and lowest in the salt sensitive variety Punjab-85.

3.3.4 Total Number of Tillers and Ears Per Plant

The decrease in the total number of tillers in saline soil ranged from 21% in LU26S to 53% in SARC-4 (Table - 3.5), but the effect of variety and variety x salinity interaction was non-significant. The effect of salinity was however highly significant.

Salinity also resulted in a significant decrease in the total number of ears per plant. This ranged from 25% in the salt tolerant variety LU26S to 57% in the salt sensitive Punjab-85. The effect of salinity was highly significant while the effects of variety and salinity x variety was non-significant in number of ears per plant also.

3.3.5 K^+, Na^+ and K^+/Na^+ Ratios in Flag Leaves

There was a very large and significant increase in Na^+ contents of flag leaves accompanied by a smaller but significant decrease in K^+ contents in all the varieties in the saline soil as compared to the normal soil (Table - 3.6).

Differences between varieties in Na^+ contents were significant on the normal as well as saline soil. Under saline conditions, significantly lowest Na^+ was recorded in the salt tolerant variety LU26S and highest values were noted in the salt sensitive variety Punjab-85. The decrease in K^+ concentration on the saline soil as compared to normal soil was significant in all the varieties except SARC-2.

K^+/Na^+ ratios were calculated from the K^+ and Na^+ data (Table - 3.6) and are presented in Table - 3.7. K^+/Na^+ ratios in the normal soil were very high. A large decrease in these ratios was noted under the saline conditions and highest values were noted in SARC-3, SARC-2 and the salt tolerant variety LU26S. In the saline soil, K^+/Na^+ ratio was statistically similar in all the varieties except SARC-3 which was similar to LU26S and SARC-2 but greater than the other varieties. In the normal soil, K^+/Na^+ ratio was highest in SARC-2 and significantly lowest in the salt-tolerant variety LU26S.

Table - 3.4: Weight (g/shoot) of main shoots and spikes (g/spike) of different wheat varieties.

Varieties	Normal soil				Saline soil				Variety means	
	Main shoots		Spikes		Main shoots		Spikes		Shoots	Spikes
	Means	± SE	Means	± SE	Means	± SE	Means	±SE		
SARC-1	1.46	0.09	2.84	0.11	0.95	0.03	2.12	0.17	1.21	2.48
SARC-2	1.64	0.18	3.03	0.16	1.29	0.10	2.63	0.09	1.47	2.83
SARC-3	1.77	0.19	3.13	0.06	0.81	0.07	1.51	0.46	1.29	2.32
SARC-4	1.69	0.16	3.21	0.17	0.90	0.12	2.33	0.36	1.30	2.77
LU26S	1.84	0.05	3.29	0.13	1.17	0.11	2.70	0.11	1.56	2.99
Punjab-85	1.37	0.08	2.80	0.12	0.61	0.07	1.51	0.37	0.99	2.16
Site means	1.63		3.05		0.94		2.13			

LSD values at p = 0.05
Site means for weight of main shoots = 0.14 (***), weight of spikes = 0.28 (***)
Variety means for weight of main shoots = 0.24 (**), weight of spikes = 0.47 (**)
V x S means for weight of main shoots = (NS), weight of main spikes = (NS)
All values are means of thirty observations.

Table - 3.5: Total number of tillers and spikes per plant.

Varieties	Normal soil				Saline soil				Variety means	
	Tillers		Spikes		Tillers		Spikes		Shoots	Spikes
	Means	± SE	Means	± SE	Means	± SE	Means	±SE		
SARC-1	8.0	0.35	7.9	0.35	4.8	0.75	4.5	0.62	6.4	6.3
SARC-2	7.9	0.59	7.9	0.59	5.1	0.40	5.1	0.40	6.5	6.5
SARC-3	6.7	0.56	6.7	0.52	4.2	0.62	3.6	0.99	5.5	5.1
SARC-4	8.3	0.59	8.3	0.59	3.9	0.29	3.6	0.29	6.1	5.9
LU26S	7.6	0.44	7.6	0.44	6.0	0.64	5.7	0.84	6.8	6.7
Punjab-85	8.1	0.29	8.1	0.29	4.1	0.19	3.4	0.37	6.1	5.8
Site means	7.8		7.8		4.7		4.3			

LSD values at p = 0.05
Site means for number of tillers = 0.61 (***), number of spikes = 0.68 (***)
Variety means for number of tillers = (NS), number of spikes = (NS)
V x S means for number of tillers = (NS), number of spikes = (NS)
All values are means of thirty observations.

Table - 3.6: Sodium and potassium contents (μ mol/g dry weight) of flag leaves in different wheat varieties.

Varieties	Normal soil				Saline soil				Var. means for potassium
	Sodium		Potassium		Sodium		Potassium		
	Means	± SE	Means	± SE	Means	± SE	Means	± SE	
SARC-1	5	0.0	632	1.3	138	1.8	610	2.9	621
SARC-2	5	0.1	804	1.6	140	2.9	798	4.3	801
SARC-3	6	0.1	790	5.7	109	0.7	721	5.7	755
SARC-4	6	0.3	662	4.5	134	5.8	533	2.9	598
LU26S	7	0.3	598	2.3	99	2.4	578	2.4	588
Punjab-85	8	0.7	791	4.0	186	2.9	777	1.0	784
Site means	6		713		134		669		

LSD values at $p = 0.05$

Na^+ :

Between varieties on normal soil = 0.75 (*)

Between varieties on saline soil = 36.6 (***)

K^+ :

Between site means = 4.32 (***)

Between variety means = 7.35 (***)

Between variety x site interaction means = 10.39 (***)

Table - 3.7: K^+/Na^+ ratios in flag leaves of different wheat varieties.

Varieties	Normal soil		Saline soil	
	Means	± SE	Means	± SE
SARC-1	123	0.5	4	0.1
SARC-2	179	1.9	6	0.1
SARC-3	134	0.4	7	0.1
SARC-4	111	6.3	4	0.2
LU26S	86	3.2	6	0.2
Punjab-85	105	9.8	4	0.1
Site means	123		5	

LSD between varieties on normal soil = 15.96 (***)

LSD between varieties on saline soil = 2.60 (**)

3.3.6 Grain Weight per Spike and Yield Components

Data showing the grain weight per spike on the normal and saline sites is presented in Table - 3.8. The variety x salinity interactions were significant for number of grains/spike and weight of grains per spike. The same interactions were non-significant for 100 grain weight, indicating that the differences between varieties were similar on the two sites. There was a significant decrease in the number and weight of grains per spike in the saline soil as compared to the normal soil. The decrease in number of grains per spike ranged from 8% in SARC-2 to 53% in SARC-3, followed by Punjab-85 (45%). The decrease in number of grains due to salt stress was also quite low in the salt tolerant variety LU26S (17%). The decrease in weight of grains ranged from 13% in SARC-2 to 52% in SARC-3. There was also a comparatively smaller decrease in grain weight in the salt tolerant variety LU26S (14%). The effects of variety were highly significant for all these three yield components. Averaged over the two sites grain weight was greatest in LU26S which was similar to SARC-2 and SARC-4 but significantly higher than SARC-1, SARC-3 and Punjab-85. Significantly lowest grain weight was noted in the salt-sensitive variety Punjab-85.

Averaged over the two sites, 100 grain weight was significantly greater in the salt-tolerant variety LU26S than SARC-1, SARC-2 and Punjab-85 and was significantly similar to the other varieties. Significantly lowest 100 grain weight was noted in Punjab-85 as compared to all the other varieties.

3.3.7 Correlation of Results

Values of the coefficient of linear correlation between weight of grains per spike and different growth parameters, sodium and potassium contents of flag leaves were calculated separately for normal and saline soils and are presented in Table - 3.9.

In normal soil weight of grains per spike was significantly and positively correlated to weight of main shoots, length and weight of spikes and number of grains per spike. Correlations with other growth parameters and K^+/Na^+ ratios of flag leaves were non-significant.

In saline soil, significant positive correlations were observed between grain weight per spike and length and weight of main shoots and spikes, number of grains per spike and number of ears per plant. All other correlations were not significant.

Table - 3.8: Grain weight per spike and yield components of different wheat varieties at normal and saline sites.

Varieties	Normal soil						Saline soil					
	Number of grains		Weight of grains(g)		100 grain weight(g)		Number of grains		Weight of grains(g)		100 grain weight(g)	
	Means	± SE	Means	± SE	Means	± SE	Means	± SE	Means	± SE	Means	± SE
SARC-1	43.7	1.36	2.16	0.09	4.99	0.09	34.0	2.20	1.68	0.12	4.93	0.03
SARC-2	46.1	3.48	2.26	0.14	4.93	0.06	42.5	2.49	1.96	0.07	4.63	0.15
SARC-3	49.4	0.46	2.42	0.06	4.93	0.09	23.3	2.41	1.16	0.39	5.54	0.28
SARC-4	46.8	4.20	2.48	0.16	5.30	0.14	36.3	1.98	1.85	0.28	5.09	0.13
LU26S	47.4	2.07	2.52	0.11	5.34	0.03	39.5	1.71	2.17	0.05	5.55	0.14
Punjab-85	48.1	1.05	2.17	0.08	4.53	0.09	26.6	2.22	1.15	0.38	4.05	0.40

Means for salinity stress

	Normal soil	Saline soil
No. of grains/ear	46.9	33.7
Wt. of grains/ear	2.33	1.66
100 Gr. wt (g)	5.00	4.96

Varietal means

	SARC-1	SARC-2	SARC-3	SARC-4	LU26S	Punjab-85
No. of grains/ear	38.8	44.3	36.3	41.5	43.4	37.3
Wt. of grains/ear	1.92	2.11	1.79	2.16	2.35	1.65
100 Gr. wt (g)	4.96	4.78	5.23	5.19	5.45	4.29

LSD values at $p = 0.05$

Site means for no. of grains/spike=4.85 (***), weight of grains/spike= 0.24 (***), 100 grain weight = 0.27 (***)

Variety means for no. of grains/ spike= 9.81 (***), weight of grains/spike= 0.41 (***), 100 grain weight = 0.46 (***)

V x S means for no. of grains/ spike =11.69 (**), weight of grains/spike= 0.58 (*), 100 grain weight = (NS)

All values are means of thirty observations.

Table - 3.9: Linear correlation coefficients between combined data for grain weight per main spike and various yield components of different wheat varieties under normal and saline soil conditions

Parameters	**Normal soil**	**Saline soil**
Flag leaf area (cm^2)	0.039 NS	-0.162 NS
Length of main shoots (cm)	0.382 NS	0.894 **
Length of main shoot spikes (cm)	0.615 **	0.824 **
Weight of main shoots (g)	0.483 *	0.606 **
Weight of main shoot spikes (g)	0.980 **	0.989 **
Number of grains per spike	0.770 **	0.964 **
100 grain weight (g)	0.405 NS	0.139 NS
Number of total tillers per plant	0.146 NS	0.422 NS
Number of ears per plant	0.140 NS	0.672 **
Sodium contents of flag leaves (μ mol/g dry weight)	0.094 NS	-0.346 NS
Potassium contents of flag leaves (μ mol/g dry weight)	-0.251 NS	-0.343 NS
K^+/Na^+ ratio in flag leaves	-0.221 NS	0.046 NS

Number of means per site for calculation of correlations = 18
NS= Non-significant at 5% level of significance
* = Significant at 5% level of significance
** = Significant at 5% level of significance

3.4 DISCUSSION

The six wheat varieties included in this study had a large variation in their tolerance to salinity (Qureshi *et al.* 1980; Ashraf and McNeilly, 1991; Niazi *et al.* 1993). The results obtained in this experiment showed a highly significant reduction in the grain weight per spike, yield components and different growth parameters as a result of salt stress.

In normal soil as well as the saline soil, LU26S gave the highest grain weight per spike comparatively and proved to be the most salt-tolerant variety even at the high soil salinity which ranged from 9.7 dS m^{-1} at booting stage to 15.8 dS m^{-1} at the time of harvesting. The better performance of LU26S might be due to its significantly higher dry weight of main shoots, better grain development and increased seed weight (expressed as the weight of 100 grains), higher spike length and spike weight as compared to all the other varieties (Francois *et al.* 1986; Srivastava *et al.* 1988; Qureshi *et al.* 1991). Variety Punjab-85 proved to be the most salt-sensitive and its dry weight of main shoots and spikes were also found to be the lowest. Grain weight of SARC-3 under saline soil conditions was almost similar to the salt-sensitive variety Punjab-85 and its dry weight of shoots and spikes was also very low and could be classified as salt-sensitive. Low dry weight of shoots and spikes was also considered a major reason for low yield in some wheat varieties grown under salt stress by Srivastava *et al.* (1988). Another major cause for low grain weight per spike in this variety was comparatively lower number of seeds per spike. Soil salinity at the booting/reproductive stage was considerably lower than the other two sampling times, which might have proved beneficial for all the varieties during the reproductive process (Maas and Poss, 1989).

Other varieties included in this study were intermediate in their grain weight per spike and could be classed as having medium salt tolerance.

As compared to the other growth parameters, salinity proved more injurious to the flag leaf area of all the wheat varieties and a decrease of about more than 50% was noted in saline soil than the normal soil. Decrease in leaf area by salinity has been reported by Srivastava *et al.* (1988). Singh *et al.* (1994) also reported that increase in salinity and RSC (sodicity) of the irrigation water increased pH of the soil but decreased flag leaf area. Flag leaf area was highest in SARC-2 in the saline soil but it did not give the highest grain weight. The linear correlation observed between grain weight and the flag leaf area was very poor on the pooled data for all the varieties (Table 3.9) in normal as well as saline soil. SARC-2 had the highest flag leaf area in the saline soil and it was also very poorly correlated with the grain weight per spike. Punjab-85 had comparatively a modest flag leaf area in the saline soil, but this was not reflected towards its grain weight under the saline soil conditions. Thorne (1982) reported that the flag leaves in wheat contribute about 82% of assimilates to the grains and hence the yield of the varieties having larger flag leaf area should be higher but the results obtained in this experiment do not support these findings.

SARC-2 was the tallest variety both under normal and saline soil conditions and it also had the longest spikes under saline soil conditions. Length of main shoots and spikes were both significantly correlated with the grain weight calculated on pooled data for all the varieties and its salt tolerance was next to LU26S. Number of spikes and tillers were also quite high in LU26S but were non-significant. Grieve *et al.* (1992) and Singh *et al.* (1994) found a similar effect of high salinity on length of tillers and spikes in wheat.

Contents of Na^+ in the flag leaves drastically and significantly increased in all the tested varieties but highest Na^+ contents were noted in the salt-sensitive variety Punjab-85 and the lowest values were observed in the salt-tolerant variety LU26S. Na^+ is a toxic ion and its diminished accumulation in LU26S and increased buildup in Punjab-85 could explain their tolerance and sensitivity to salinity respectively. In the pooled data for all the varieties, there was a poor correlation between grain weight per spike and Na^+ contents of the flag leaves (Table - 3.9). Schachtman and Munns (1992) reported that salt-tolerant *Triticum* species had lower rate of Na^+ accumulation than the salt-sensitive ones. The mechanism of Na^+ uptake was argued to be regulated by root processes and the processes of ion compartmentation within the leaves which enhances the ability to tolerate high concentrations of Na^+ in the leaves. On the basis of their experiments in greenhouse and field, Qureshi *et al.* (1993) concluded that different cultivars may adopt different mechanisms for tolerating high external salinity. The exclusion of Na^+ and Cl^-, high RGR for compensating for high Na^+ uptake or selective uptake of Na^+ and K^+ and their compartmentation away from the growing tissues can be important mechanisms for salt tolerance in different wheat genotypes. Excessive Na^+ and Cl^- uptake by the plants may disturb the uptake of K^+ and other nutrient elements (Munns and Termaat, 1986), especially NO_3^- which in turn may depress the growth and adversely affect the yield and different yield components.

A significant decrease occurred in all the varieties in K^+ contents of flag leaves under saline soil conditions. Storey and Wyn Jones (1978) also reported that NaCl salinity decreases K^+ concentration in many species e.g. barley. K^+ concentration in xylem sap was reported to decline when the external NaCl concentrations reached 100 mol m^{-3} (Munns and Termaat, 1986). In spite of a significant decrease in K^+ in the saline soil in different varieties, K^+ concentration was 4-6 times more than the Na^+ contents. This high selectivity of K^+ is an important physiological mechanism for plant survival in saline environments (Wyn Jones *et al.* 1979). This mechanism was more evident in salt-tolerant variety LU26S and least in the salt-sensitive variety Punjab-85. This decrease in K^+ contents ranged from 1-19% in different varieties, highest decrease being noted in SARC-4. Sharma *et al.* (1994) concluded that greater dry matter accumulation, K^+ and nitrogen contents and reduced uptake of Na^+ and Cl^- as characters for salt resistance and suggested that these characters could be used as a criteria for rapid screening programmes for different crops. In this study, there was a reduced uptake of Na^+ in the saline soil in LU26S which is a salt-tolerant variety. K^+ uptake also decreased under saline conditions but there was not a clear trend in this case. In the saline soil, there was mostly a high positive linear correlation between the grain weight per spike and K^+ contents of the flag leaves in all the varieties.

K^+/Na^+ ratio was quite high in the salt-tolerant variety LU26S in the saline soil (Table - 3.7) which might also be an other reason for its better salt tolerance. In the salt-sensitive variety Punjab-85, K^+/Na^+ ratio in saline soil was among the lowest of all the varieties. On the basis of these results, it may be suggested that this ratio may serve as an other criteria for salt tolerance in wheat genotypes. However, in this study it was poorly correlated with the grain weight (Table - 3.9) in pooled data for all the varieties. Maliwal and Sutaria (1992) conducted an experiment on five wheat varieties in pots having salinized soil at 4.05, 8.05, 15.40 dS m^{-1}. The results showed that the K^+/Na^+ ratio was the highest in the salt-tolerant variety Kharchia-69. They found significant negative correlations between grain yield and the concentration of Na^+ of cell sap and suggested that this could be used for judging salt tolerance in wheat.

. The results of this study suggest that exclusion of excessive Na^+ and other toxic ions like Cl^- (data not presented) in the leaves of salt-tolerant variety LU26S could also be a reason for its ability to maintain a higher yield in the saline soil, although there were poor and non-significant correlation of flag leaf Na^+ concentrations (pooled data for six varieties) and grain weight per spike. Gorham (1993) concluded that salt tolerance in crops such as wheat and barley is largely determined by their ability to exclude Na^+ and Cl^- from their shoots and their ability to maintain high shoot K^+ concentrations.

3.5 CONCLUSIONS

LU26S proved to be the most salt-tolerant variety and gave the highest grain weight under saline conditions possibly due to its low Na^+ uptake, high K^+/Na^+ ratio, higher dry weight of shoots and spikes and better grain development (100 grain weight). Better exclusion of Na^+ and other ions from the leaves of salt-tolerant variety LU26S could also be a reason for its ability to maintain a higher grain weight in the saline soil. High Na^+ uptake, lower K^+/Na^+ ratio, lower dry weight of main shoots and spikes and lower 100 grain weight were the main reasons for salt-sensitivity in Punjab-85.

Flag leaf area decreased drastically due to salt stress in all the varieties and this could be a major cause for low yield in the saline soil. There was however, a very low linear correlation between the flag leaf area and the grain weight in pooled data for all the six wheat varieties.

This experiment was conducted on a saline soil using six wheat varieties. To examine the effects of sodic soil on wheat varieties under field conditions, another experiment was conducted and its results are reported in the following chapter.

CHAPTER 4

GRAIN YIELD, ION UPTAKE AND NET PHOTOSYNTHESIS OF SOME WHEAT VARIETIES DIFFERING IN SALT-TOLERANCE GROWN UNDER SODIC FIELD CONDITIONS IN PAKISTAN

CHAPTER 4

GRAIN YIELD, ION UPTAKE AND NET PHOTOSYNTHESIS OF SOME WHEAT VARIETIES DIFFERING IN SALT-TOLERANCE GROWN UNDER SODIC FIELD CONDITIONS IN PAKISTAN

4.1 INTRODUCTION

The experiment reported in chapter 3 was conducted under saline soil conditions. Another major type of salt stress is encountered in 'sodic soils'. These will have a high exchangeable sodium percentage but contain lower concentrations of soluble salts. The exchangeable sodium percentage (ESP) of the soil is always more than 15 and electrical conductivity of the saturation extract (EC_e) from these soils is always less than 4 dS m^{-1}. Due to the high sodium hazard, the pH of the soil is always more than 8.5. Crop plants growing in these soils suffer mostly due to excessive sodium and poor physical conditions of the soil and less due to an osmotic effect (Richards, 1969). Management and crop production from this type of soil is a major problem in central parts of Pakistan and elsewhere in many parts of the world. These soils develop from saline soils after precipitation of excess Ca^{2+} as $CaSO_4$ and leaching of excess salts, which results in an increase in the proportion of Na^+ in the soil and followed by increased ESP (Richards, 1969). Sustained use of sodic and saline sodic waters also results in increased pH and ESP of the soil, thus turning the normal soil into a 'sodic soil' and has a detrimental effect on the crop yields (Bajwa *et al.* 1993). Gupta and Sharma (1990) evaluated experimental data for 20 crops for their tolerance to sodicity and found that *Sesbania aculeata*, rice and wheat had comparatively greater tolerance to sodicity and among wheat varieties, Kharchia-65 appeared to be the most tolerant. Yasin (1991) reported a decrease in grain and straw yields of wheat varieties at 38.5 and 56.4 ESP of the soil with an increase in plant Na^+ and decrease in K^+ contents. Sharma (1991) reported that the cultivars resistant to sodicity maintained higher leaf Na^+ concentrations and lower Na^+/K^+ ratios than the sensitive cultivars. Similar results were reported by Schatchtman and Munns (1992) for wheat genotypes grown under saline conditions. In a greenhouse experiment conducted on wheat by Padole (1991), it was found that combined effects of salinity and sodicity were greater than salinity alone and that uptake of N, P, K, Ca^{2+}, Mg^{2+}, Zn^{2+}, Fe^{2+}, Cu^{2+} and Mn^{2+} were reduced by salinity and/or sodicity of soil and irrigation water. Srivastava and Srivastava (1993) studied pH dependent changes in iron availability in rice and wheat plants and reported that with the rise in pH from 7.2 to 10.3, water soluble and exchangeable Fe^{2+} decreased while levels of iron oxide increased. Gas exchange in wheat has been reported to be affected by accumulation of excess Na^+ and Cl^- in different plant species after exposure to NaCl salinity (Downton, 1977; Walker *et al.* 1982; Kaiser, 1984; Terry and Waldron, 1984; Yeo *et al.* 1985; Rawson, 1986; Kemal-ur-Rahim, 1988; Leidi and Lips, 1990; Kalaji and Nalborczyk, 1991; Bethke and Drew, 1992; Iqbal, 1992) but relevant data for wheat on sodic soils under field condition is scanty. In a pot study on rice and wheat using soils having ESP 18 and 34, Hussain *et al.* (1994) found that with increasing ESP wheat straw yield and productive tillers in both the crops were not affected but grain yield of both these crops decreased by increasing ESP. Khan (1996) reported that there was no significant decrease in Pn of wheat with increase in ESP of the soil. In a pot study, Singh *et al.* (1990) reported that in *brassica* plants, Pn, E, g_s , chlorophyll content and leaf area per plant were decreased by soil sodicity.

This field experiment was conducted on a dense, sodic soil at the Saline Agriculture Station of Pakistan Agricultural Research Council, Islamabad, Pakistan. The purpose was to study the comparative yield potential of different wheat varieties having variable degrees of salt tolerance and to correlate the yield with carbon assimilation rate and potassium and sodium contents of flag leaves. The measurements were made on flag leaves because these have been reported to contribute about 82% of assimilates to the grains (Thorne, 1982). Another aim was to select two or three suitable varieties for more detailed glass house studies in the UK, according to their performance in the field.

4.2 MATERIALS AND METHODS

4.2.1 Experimental Material

4.2.1.1 Wheat seeds

Ten wheat varieties were selected for this experiment including the four previously studied at the University of Wales, Bangor, UK (see Chapter 2) and the six varieties studied at the saline site in Pakistan (see Chapter 3). The seeds were collected from Soil Science Department (Saline Agriculture Programme), University of Agriculture, Faisalabad, Pakistan. The names of these varieties and their reported salt tolerance are given below.

1. SARC-1 Moderately tolerant to tolerant (Qureshi, R. H. 1997, Pers. Communication)
2. SARC-2 Moderately tolerant (Qureshi, R. H. 1997, Pers. Communication)
3. SARC-3 Moderately tolerant (Qureshi, R. H. 1997, Pers. Communication)
4. SARC-4 Moderately tolerant (Qureshi, R. H. 1997, Pers. Communication)
5. LU26S Salt tolerant (Ashraf and McNeilly, 1991; Qureshi *et al.* 1993)
6. Punjab-85 Salt sensitive (Ashraf and McNeilly, 1991; Qureshi *et al.* 1993)
7. Pato Salt sensitive (Akhtar *et al.* 1994)
8. 7-Cerros Moderately tolerant (Hollington *et al.* 1992)
9. PAK-81 Moderately tolerant (Qureshi *et al.* 1993)
10. Kharchia-65 Salt tolerant (Sharma, 1989)

4.2.1.2 The Soil and Soil Preparation

The experiment was conducted at Saline Agriculture Research Station, Sadhuke, Pakistan at two adjacent sites which were about 200 metres apart. One site was a 'normal' soil ($EC_e < 4.0$; pH < 8.5 and ESP < 15.0) which had been previously reclaimed with gypsum. The soil was classed as a non-saline soil according to the criteria of United States Department of Agriculture (Richards, 1969). The other site was a dense 'sodic' soil ($EC_e < 4.0$, pH > 8.5 and ESP > 15.0). The texture of the soil at both the sites was clay loam. Crop rotation followed at the farm was wheat-rice-wheat. All ten varieties were sown at both sites. Soil samples (0-15 cm) were collected at sowing, booting and harvest. Twenty, 500g soil samples were collected randomly from each site using a soil auger and mixed thoroughly. Composite samples weighing about 1 kg were taken from these bulk samples, dried in air, ground, sieved through a 2mm sieve and put in plastic bags for analysis. These were analysed to assess the nature and magnitude of the stress using the analytical procedures described by Richards (1969). The detailed physico-chemical analysis is presented in Table - 4.1. The soil was irrigated and when in the proper moisture condition, a fine seed bed was prepared for sowing the seed. The first soil sampling was done at this time and before fertilizer application to assess the nature and magnitude of the salt stress. Fertilizer was applied at the rate of 80 kg N ha^{-1}, 70 kg P_2O_5 ha^{-1} and 50 kg K_2O ha^{-1}. Half the amount of nitrogen and the full rate of phosphorus and potassium was applied at the time of seed bed preparation. The remaining half of the nitrogen was applied at the time of the second irrigation. Soil samples were collected again at the time of booting and harvest (Table-4.1).

Table - 4.1: Physico-chemical soil characteristics (electrical conductivity of saturation paste extract in dS m^{-1} (EC_e), pH of saturation paste, soluble carbonates (CO_3^{2-}), bicarbonates (HCO_3^-), chlorides (Cl^-), calcium plus magnesium ($Ca^{2+}+Mg^{2+}$), sodium (Na^+), sodium adsorption ratio (SAR) and exchangeable sodium percentage (ESP).

Time of sampling	EC_e dS m^{-1}	pH	CO^{3-}	HCO^{3-}	Cl^-	$Ca^{2+}+Mg^{2+}$	Na^+	SAR	ESP *
Normal soil	(0-15 cm)								
Sowing	2.8	8.6	Traces	5.0	15.4	5.4	21.4	13.2	15.0 (14.7)
Booting	2.9	8.5	-	11.1	4.4	6.8	23.3	12.6	14.8 (14.7)
Harvest	1.3	8.3	-	7.0	3.5	6.0	12.6	7.3	8.7 (9.2)
Sodic soil	(0-15 cm)								
Sowing	3.4	9.6	3.0	7.0	9.8	4.0	28.0	19.8	21.8 (22.2)
Booting	4.0	9.7	5.0	10.5	7.1	8.3	31.5	15.5	17.7 (19.3)
Harvest	3.1	8.7	Traces	2.5	8.7	6.0	26.7	15.4	17.7 (19.1)

* ESP within the parenthesis are actual values obtained through laboratory assay of exchangeable Na^+. ESP values outside the parenthesis were calculated from SAR data.

* Concentrations of CO_3^{2-}, HCO_3^-, Cl^-, Ca^{2+} + Mg^{2+} and Na^+ are in meq. per litre (me l^{-1}).

The normal soil was a non-saline soil and its EC_e further decreased with the passage of time due to leaching of the salts to lower horizons. At the time of harvest, it had dropped to 1.3 dS m^{-1}. Apart from EC_e, there were large reductions in pH, chloride and sodium contents and ESP of the soil towards the end of the experiment. Contrary to these, there was a slight increase in Ca^{2+}+Mg^{2+} contents.

The stressed soil was a sodic soil with marginal salinity but even then its EC_e was higher than the normal soil. At all the sampling stages, EC_e did not go higher than 4.0 dS m^{-1}. There was a decrease in pH with the passage of time but even then, at the time of harvest, it was higher than 8.5. ESP also decreased but at the time of last sampling, it remained higher than 15.0. The data showed that at all the three growth stages, the soil remained a sodic soil ($EC_e < 4.0$, pH > 8.5 and ESP > 15.0) in spite of some decreases in pH, sodium and ESP. The soil had some degree of spatial variability at this site and the data for soil analysis reported in Table-4.1 are from a soil sample composited from 20 soil samples collected randomly from different parts of the field. Spatial variability in salt affected fields has been reported to be usually very high by Igartua (1995).

4.2.1.3 Sowing

At each site, the experiment was laid out according to randomized complete block design with three replications. The crop was sown on 17 November, 1993 using a single row cotton drill at a seed rate of 50 kg/ha. Each block was divided into 10 plots. Each plot was assigned to one variety and was 12 m long and consisted of 5 rows spaced 30 cm apart.

4.2.2 Maintenance of the Experiment

After germination, thinning was done and plant to plant distance was maintained at about 2.5 cm. Plots at both sites were supplied with water. Six irrigations were given with non-saline tube well water and light rains were received four times during the period of the experiment. The crop remained free of any insect and disease attack. Hand hoeing was done after the first and second irrigations to eradicate weeds.

4.2.3 Visual Observations

Plant mortality was noted in all the varieties at the sodic site. Due to the dense and sodic nature of the soil in this block, irrigation water remained standing on the soil surface for 5-6 days after every irrigation which proved harmful for the crop. As a result, the crop growth in the sodic site remained stunted and the crop matured about one week earlier than the normal block.

4.2.4 Growth and Gas Exchange Measurements

4.2.4.1 Flag Leaf Area

Five flag leaf samples were taken from each plot at the time of anthesis. Flag leaf area was calculated using the following formula as described in section 2.2.6 (Chapter - 2).

Leaf area = (0.9 x Length)x(0.5 x maximum width) .... (Robson and Sheehy, 1980).

4.2.4.2 Gas Exchange Measurements

Gas exchange of flag leaves was recorded during the grain filling stage in four varieties (SARC-1, PAK-81, LU26S and Kharchia-65) using a portable Infra Red Gas Analyzer (Model LCA 3, Analytical Development Company, Ltd. Pindar Road, Hoddesdon, Herts, UK). It was originally intended to make measurements on all varieties but this was not possibly due to a failure of the stirrer fan motor in the leaf chamber. These measurements were made on 24 and 25 March, 1994 (127 DAS) on 10 flag leaves in each replication from each treatment (normal and sodic site) and variety. Gas exchange parameters were measured on fully expanded, attached, healthy looking flag leaves with minimum visible symptoms of senescence to reduce interplant variability and compare leaves of similar physiological age. These data were recorded under ambient day light conditions at a mean photosynthetic photon flux density (PPFD) of $1410 \pm 26.4\ \mu mol\ m^{-2}\ s^{-1}$. The columns of dry silica gel in the IRGA were changed before starting the measurements on each day and in between the measurements after its colour changed from blue to green. The IRGA was kept under the shade of a big umbrella to save the electrical components from malfunctioning due to high ambient temperature and only the leaf chamber was kept in the sun light during the measurements.

The telescopic tube for the air supply to the air pump was fixed about 3 metres high above the crop canopy to ensure an air supply of uniform composition.

About fifteen minutes prior to gas exchange measurements, the air supply unit, IRGA and

PLC were switched on to purge the system and to bring the IRGA and PLC up to their operating temperature. A constant volume flow rate of 500 cm^3 min^{-1} dry air into the cuvette in the IRGA from the volumetric air supply unit was maintained.

The leaf chamber model (PLCA) with variable leaf area (max. 10cm^2) was used for wheat which is considered suitable for cereals and grasses. The Parkinson leaf chamber (PLC) was clamped over the central portion of the leaf with the adaxial side of the leaf uppermost and held in such a way so as to get the maximum light on the leaf surface and so as to avoid shading by any of the other leaves.

The time required for each measurement from the close of the hand held leaf chamber to the display of the final results on the LCD of the data logger was about 30 seconds and data was recorded in the data logger when the values in the data display became constant. Preliminary investigations (Parkinson leaf chamber manual, ADC; Iqbal, 1992) reported that 30 seconds were adequate to purge the system so that initial steady readings of carbon exchange rate and other parameters were obtained before the stomata started to close.

4.2.4.3 Transfer and Analysis of Data

A set of records consisting of inputs from the key board, inputs from the LCA and calculated parameters were stored in the data-logger. The data recorded during two days was later downloaded on to a floppy disk at the National Agricultural Research Centre, Islamabad, Pakistan, using a transfer program written in Qbasic language which was later on imported into a Quattro Pro spreadsheet. The data was then later transferred to the main frame computer at the University of North Wales, Bangor into Minitab statistical package for statistical manipulations.

4.2.4.4 Potassium and Sodium Estimations

Thirty flag leaves (10 from each replication) were collected from each treatment and variety at the same time as the gas exchange measurements were made to determine cation concentrations. These were stored in labelled paper bags and were dried in an oven at 70° C for 72 hours and weighed.

The leaves were extracted in 20 ml. pyrex test tubes in 10 ml of 0.1 M acetic acid at 80° C in a water bath for 1.5 hours. The whole leaf was kept submerged in the acetic acid to ensure proper extraction. The test tubes were covered tightly with cling film to avoid any evaporation and changes in the concentration of extracted ions.

The concentrations of sodium and potassium in this extract were measured by atomic absorption spectrophotometer (Pye Unicam Model SP-919) at the School of Biological Sciences, University of Sussex, Brighton. These results were used to determine the concentrations per unit leaf dry weight.

4.2.4.5 Grain Weight per spike and Yield Components

To determine yield and yield components, thirty plants (10 from each replication) were harvested by cutting at the soil surface from each treatment and variety at maturity on 24 and 25 April, 1994 (157 DAS). The following data were recorded from these plants.

i. No. of tillers per plant
ii. No. of ears per plant
iii. Length of main shoots and spikes (cm)
iv. Total weight of main shoots and spikes (g)
v. Number of grains in the main shoot spike.
vi. Weight of grains per main spike (g)
vii. 100 grain weight (g)
viii. Grain yield per square metre (g)

To calculate the yield on square metre basis, a metre length of crop was harvested from three different rows from each plot. The plants were weighed and threshed. The grains were weighed and the data was converted to grams per square metre.

4.2.5 Statistical Analysis

The data for the two sites were combined and analysed using analysis of variance according to the procedure for experiments repeated over different sites; described by Cochran & Cox (1957) using Minitab statistical package for Windows v. 10.2. Two examples of the anova tables are presented in Appendix - 4.1 and 4.2. The least significant differences (LSD) of the means were worked out by the equation described in Chapter 2 (section 2.2.8).

There were large differences in Na^+ and K^+/Na^+ of the flag leaves in normal and sodic soils, hence LSD and anova were calculated separately for both of these soils for these two parameters (see Chapter 3, section 3.2.5).

4.3 RESULTS

4.3.1 Flag Leaf Area

Flag leaf area (FLA) of the different wheat varieties was recorded at the time of anthesis and the data are presented in Table - 4.2. There were no significant differences in flag leaf area between varieties. The effect of site was highly significant. However, the variety x site interaction was non-significant.

There was a significant decrease in leaf area under sodic conditions in all the varieties tested. Under normal soil conditions, highest flag leaf area was exhibited by PAK-81 (moderately salt-tolerant) while the lowest area was noted in SARC-4. However overall differences in FLA between varieties were not statistically significant. The decrease in leaf area under sodic conditions, varied between approximately 44% and 62% in different wheat varieties. Depression in leaf area was least in SARC-2 (44%) followed by 7-Cerros (50%), SARC-1 (52%) and the salt tolerant variety LU26S (52%). The depression was greatest in the salt tolerant variety Kharchia-65 (62%). The decrease in flag leaf area in the salt sensitive variety Punjab-85 was also very high under sodic conditions (59%).

4.3.2 Gas Exchange Rate

Net Photosynthesis (Pn), transpiration rate (E), stomatal conductance (g_s), leaf temperature and sub-stomatal CO_2 were recorded in SARC-1, LU26S, PAK-81 and Kharchia-65 at a mean light level of (PPFD) 1410 ± 26.4 μmol m^{-2} $second^{-1}$ at 127 DAS (Tables - 4.3, 4.4 and 4.5). With the exception of leaf temperature, there was a marked decrease in all these physiological parameters under sodic soil conditions. Under normal soil conditions, Pn was significantly higher in SARC-1 and PAK-81, both of which are reported to be moderately salt tolerant, than in LU26S and Kharchia-65. Under sodic conditions, photosynthetic rate was significantly higher in LU26S (salt tolerant) than in all other varieties. The depression in Pn due to soil sodicity was significant in all varieties except LU26S. Pn was lowest in Kharchia-65 and highest in LU26S under sodic soil conditions. Transpiration rates were similar in all the four varieties under normal soil conditions. Under sodic conditions, highest transpiration rates were noted in case of PAK-81 and LU26S. Transpiration rate in SARC-1 and Kharchia-65 were similar under salt stress. Generally stomatal conductance was considerably decreased under sodic conditions. Stomatal conductance was the highest in PAK-81 under normal as well as sodic

Table- 4.2: Flag leaf area (cm^2) of different wheat varieties.

Varieties	Normal soil		Sodic soil		Variety means
	Means	± SE	Means	± SE	
SARC-1	17.4	1.10	8.4	0.74	12.9
SARC-2	16.4	1.11	9.1	0.53	12.7
SARC-3	18.4	0.77	8.6	0.79	13.5
SARC-4	15.9	0.61	7.2	0.68	11.6
LU26S	17.7	1.06	8.5	0.69	13.1
Punjab-85	17.6	0.89	7.1	0.38	12.4
Pato	18.2	1.29	8.3	0.66	13.2
7-Cerros	17.1	1.16	8.5	0.68	12.8
PAK-81	19.2	1.16	8.0	0.62	13.6
Kharchia-65	17.6	0.96	6.6	0.53	12.1
Site means	17.5		8.0		

LSD values at p= 0.05

Site means = 0.89 (***); Variety means = (NS); Variety x site means = (NS)
All values (Variety x site) are means of fifteen observations.
All values for variety and site means are averages of 30 and 150 observations.

Table - 4.3: Effect of salt stress on net photosynthesis (Pn; μmol m^{-2} s^{-1}) in four wheat varieties.

Varieties	Normal soil		Sodic soil		Variety means
	Means	± SE	Means	± SE	
SARC-1	15.5	0.4	10.3	0.1	12.9
LU26S	12.6	0.6	11.8	0.1	12.2
PAK-81	15.2	0.1	10.7	0.3	12.9
Kharchia-65	12.9	0.4	9.9	0.1	11.4
Site means	14.1		10.7		

LSD values at p = 0.05

Site means for Pn = 0.46 (***)
Variety means for Pn = 0.65 (***)
Variety x site means for Pn = 0.93 (***)
All variety x site, variety and site values are means of twenty, forty and eighty observations.

Table - 4.4: Effect of salt stress on transpiration (E; mmol m^{-2} s^{-1}), stomatal conductance (g_s; mol m^{-2} s^{-1}) in four wheat varieties.

Varieties	Normal soil				Sodic soil				Variety means	
	E		g_s		E		g_s		E	g_s
	Means	± SE	Means	± SE	Means	± SE	Means	± SE		
SARC-1	7.3	0.1	0.29	0.007	4.6	0.1	0.12	0.002	5.9	0.21
LU26S	7.0	0.5	0.26	0.006	5.7	0.1	0.16	0.005	6.3	0.21
PAK-81	7.1	0.2	0.31	0.006	5.8	0.1	0.17	0.006	6.4	0.24
Kharchia-65	7.1	0.3	0.26	0.011	4.7	0.2	0.14	0.010	5.9	0.20
Site means	7.1		0.28		5.2		0.15			

LSD at p = 0.05
Site means for E = 0.37(***), g_s = 32.14 (***)
Variety means for E = (NS), g_s = (NS)
Variety x stress means for E = 0.74 (*), g_s = (NS)
All variety x site, variety and site values are means of twenty, forty and eighty observations.

Table - 4.5: Effect of salt stress on sub-stomatal carbon dioxide (Ci; $\mu l\, l^{-1}$) and Leaf temperature (°C) in four wheat varieties.

Varieties	Normal soil				Sodic soil				Variety means	
	Leaf temperature		Ci		Leaf temperature		Ci		Leaf temp.	Ci
	Means	± SE	Means	± SE	Means	± SE	Means	± SE		
SARC-1	32.9	0.10	194	3.8	34.7	0.36	164	5.6	33.4	178
LU26S	34.2	0.33	206	6.5	35.3	0.23	167	4.1	34.8	186
PAK-81	32.4	0.35	203	4.9	34.5	0.18	195	2.8	33.4	199
Kharchia-65	33.4	0.10	210	3.4	33.4	0.51	177	8.8	33.8	194
Site means	33.2		203		34.5		176			

LSD at p = 0.05
Site means for Ci = 13.11 (***), Leaf temperature = 0.87 (**)
Variety means for Ci = (NS), Leaf temperature = (NS)
Variety x site means for Ci = (NS), Leaf temperature = (NS)
All variety x site, variety and site values are means of twenty, forty and eighty observations.

conditions. Stomatal conductance decreased least in LU26S (37%) and greatest in SARC-1 (60 %). The lowest g_s was observed in Kharchia-65 showing a decrease of about 51% as compared to control. There was a slight increase in leaf temperature in all the varieties under sodic conditions which varied between 3 and 7%. In Kharchia-65 however, the leaf temperature remained the same as observed in normal soil. Sub-stomatal CO_2 (Ci) decreased under sodic conditions in all the varieties and highest decrease was noted in LU26S (18%) and SARC-1 (18%) while the lowest decrease was noted in PAK-81 (7%).

The effects of sites were significant to highly significant for all the measured gas exchange parameters. Variety means were only significant for Pn and were non-significant for all other parameters. Effects of variety x site were non- significant for all parameters except Pn where these were highly significant ($p<0.001$).

4.3.3 Length of Main Shoots and Spikes

Data presented in Table-4.6 show that SARC-2, SARC-3, 7-Cerros and Kharchia-65 were tall varieties while SARC-1 and PAK-81 were short ones. The effects of variety, site and variety x site were highly significant for both length of spikes. In case of length of main shoots, effects of variety were significant while their interaction was non-significant. There was a significant decrease in the length of the main shoot in all the varieties under sodic conditions. The magnitude of this decrease varied between 28% and 38% in different varieties; the greatest decreases being noted in SARC-2 and SARC-3 and the least in PAK-81. Spike length was greatest in SARC-2 and SARC-3 in normal soil while in the sodic soil, the spike length was highest in 7-Cerros followed by SARC-3 and SARC-2. The shortest spikes were found in Pato in normal soil. Under sodic soil conditions, there was a significant decrease in spike length in all the varieties. The magnitude of the decrease in the spike length varied between 9 and 30% in different varieties. The decrease was least in Pato and greatest in PAK-81. Under sodic conditions, the longest spikes were found in 7-Cerros followed by SARC-3 and SARC-2; while the shortest spikes were found in salt tolerant Kharchia-65 in which spike length was decreased by 30%.

4.3.4 Weight of Main Shoots and Spikes

Weight of main shoots and spikes at the time of harvest is presented in Table-4.7. The

Table - 4.6: Mean length (cm) of main shoots and spikes.

Varieties	Normal soil				Sodic soil				Variety means	
	Main shoots		Spikes		Main shoots		Spikes		Shoot	Spikes
	Means	± SE	Means	± SE	Means	± SE	Means	± SE		
SARC-1	80.3	1.2	10.9	0.3	54.3	1.1	9.8	0.3	67.3	10.4
SARC-2	106.0	1.8	12.1	0.2	65.5	1.2	10.0	0.2	85.8	11.1
SARC-3	107.0	1.1	12.5	0.2	65.8	1.9	10.4	0.2	86.2	11.4
SARC-4	98.3	1.5	11.4	0.2	63.1	1.2	9.5	0.2	80.7	10.5
LU26S	98.3	0.9	11.9	0.3	63.2	1.7	9.8	0.2	80.7	10.8
Punjab-85	92.6	0.8	10.3	0.2	56.3	1.8	9.2	0.2	74.5	9.7
Pato	94.4	1.4	9.7	0.2	63.3	1.9	8.9	0.2	78.8	9.3
7-Cerros	100.0	1.2	11.5	0.2	71.1	1.0	10.6	0.2	85.7	11.0
PAK-81	88.8	1.4	11.8	0.2	64.3	1.2	8.1	0.3	76.6	10.0
Kharchia-65	102.0	1.5	11.5	0.3	65.3	1.2	8.0	0.3	83.6	9.8
Site means	96.8		11.4		63.2		9.4			

LSD at $p = 0.05$
Site means for length of main shoots = 3.11 (***), length of spikes = 0.39 (***)
Variety means for length of main shoots = 6.89 (***), length of spikes = 0.88 (***)
Variety x site means for length of main shoots = (NS), length of spikes = 1.24 (*)
All values are means of thirty observations.

Table - 4.7: Mean weight (g/shoot) of main shoots and spikes of different wheat varieties.

Varieties	Normal soil				Sodic soil				Variety means	
	Main shoots		Spikes		Main shoots		Spikes		Shoots	Spikes
	Means	± SE	Means	± SE	Means	± SE	Means	± SE		
SARC-1	1.68	0.06	2.50	0.12	0.84	0.04	1.74	0.15	1.26	2.12
SARC-2	2.01	0.07	3.17	0.10	0.88	0.04	1.85	0.09	1.45	2.51
SARC-3	2.21	0.07	3.42	0.12	1.06	0.06	2.03	0.17	1.63	2.72
SARC-4	1.89	0.06	2.73	0.11	0.94	0.05	2.06	0.13	1.41	2.40
LU26S	2.02	0.07	3.17	0.15	0.96	0.05	2.13	0.16	1.49	2.65
Punjab-85	1.87	0.06	3.04	0.12	0.86	0.04	2.03	0.14	1.37	2.52
Pato	1.50	0.05	2.37	0.09	0.90	0.05	1.74	0.11	1.20	2.06
7-Cerros	2.28	0.07	3.73	0.11	1.43	0.05	2.94	0.09	1.85	3.34
PAK-81	2.32	0.07	4.47	0.14	0.96	0.06	1.86	0.12	1.64	3.17
Kharchia-65	1.68	0.08	2.52	0.15	0.77	0.05	1.48	0.11	1.22	2.00
Site means	1.15		3.11		0.96		1.98			

LSD at p = 0.05

Site means for weight of main shoots = 0.09 (***), weight of spikes = 0.23 (***)

Variety means for weight of main shoots = 0.20 (***), weight of spikes = 0.51 (***)

Variety x site means for weight of main shoots = 0.28 (*), weight of main spikes = 0.73 (*)

All values are means of thirty observations.

effects of variety, site and the variety x site interaction were highly significant for weight of main shoots and spikes. Main shoot weight was highest in PAK-81 and 7-Cerros and lowest in Pato and SARC-1 under normal soil conditions. A significant decrease in weight of main shoots was noted under sodic soil conditions in all the varieties. Spike weight in normal soil was also greatest in PAK-81 and 7-Cerros. There was a marked and significant decrease in spike-weight under sodic conditions in all the varieties. Spike weight was lowest in Kharchia-65 and highest in 7-Cerros and LU26S (salt tolerant variety) in sodic soil.

4.3.5 Total Number of Tillers and Spikes Per Plant

For total number of tillers per plant, the effects of variety and site were significant. In number of spikes, the effect of site was significant while that of variety was non-significant. Variety x site interactions were non-significant for both number of tillers and number of spikes. Total number of tillers and spikes decreased significantly under sodic soil conditions (Table-4.8). The highest numbers of tillers and spikes were found in SARC-1 and 7-Cerros. The decrease in total number of tillers per plant varied between 25% and 48% and for spikes between 34 and 53%. The largest decrease in total number of tillers was found in SARC-1 while the smallest decrease was noted in 7-Cerros. Number of spikes per plant were decreased least in SARC-2, SARC-4 and most in PAK-81, Kharchia-65 (salt tolerant variety) and Punjab-85 (salt sensitive variety) under the sodic soil conditions.

4.3.6 Sodium (Na^+), Potassium (K^+) and K^+/Na^+ Ratios in the Flag Leaf

Data regarding sodium and potassium in the flag leaf of different wheat varieties is presented in Table-4.9. There was a very large and significant increase in sodium and a smaller but significant decrease in potassium contents in the flag leaves of all the varieties in sodic soil as compared to normal soil. There were large differences in sodium and K^+/Na^+ ratios in the sodic soil as compared to the normal soil. The site, variety and variety x site interactions were significant for K^+. Varieties differed significantly in their Na^+ and K^+/Na^+ ratios separately under normal as well as sodic soil.

Differences in Na^+ concentrations between varieties were significant in normal as well as sodic soil. Na^+ concentrations in SARC-1, SARC-2, Punjab-85, and Pato were significantly higher than in SARC-3, 7-Cerros, PAK-81 and Kharchia-65 in the sodic soil. In normal soil, highest

Table - 4.8: Total number of tillers and spikes per plant

Varieties	Normal soil				Sodic soil				Variety means	
	Tillers		Spikes		Tillers		Spikes		Tillers	Spikes
	Means	± SE	Means	± SE	Means	± SE	Means	± SE		
SARC-1	5.07	0.34	4.27	0.31	2.63	0.16	2.37	0.16	4.03	3.50
SARC-2	4.17	0.25	3.60	0.32	2.70	0.22	2.37	0.24	3.43	2.98
SARC-3	4.43	0.29	4.20	0.25	3.03	0.23	2.33	0.23	3.73	3.27
SARC-4	4.07	0.27	3.67	0.26	2.87	0.26	2.43	0.24	3.47	3.05
LU26S	4.63	0.26	4.27	0.29	2.57	0.20	2.13	0.18	3.60	3.20
Punjab-85	4.17	0.24	3.77	0.25	2.67	0.22	2.10	0.20	3.42	2.93
Pato	4.63	0.22	3.93	0.26	3.30	0.23	2.57	0.27	3.97	3.25
7-Cerros	5.00	0.28	4.47	0.31	3.73	0.21	2.77	0.24	4.37	3.62
PAK-81	4.43	0.31	4.20	0.32	2.80	0.15	1.97	0.11	3.62	3.08
Kharchia-65	4.17	0.32	3.40	0.26	2.50	0.13	1.93	0.14	3.33	2.67
Site means	4.51		4.01		2.88		2.30			

LSD at $p = 0.05$
Site means for number of tillers = 0.27 (***), number of spikes = 0.27(***)
Variety means for number of tillers = 0.60 (*), number of spikes = (NS)
Variety x site means for number of tillers = (NS), number of spikes = (NS)
All values are means of thirty observations.

Table - 4.9: Sodium (Na^+) and potassium (K^+) contents (μ mol/g dry weight) of flag leaves in different wheat varieties.

Varieties	Normal soil				Sodic soil				Variety means
	Na^+		K^+		Na^+		K^+		K^+
	Means	± SE	Means	± SE	Means	± SE	Means	± SE	
SARC-1	5	0.16	436	18.1	419	7.9	341	23.3	338
SARC-2	10	0.57	534	17.8	431	48.5	458	74.0	496
SARC-3	6	0.33	532	15.4	320	9.6	504	14.1	518
SARC-4	9	0.63	435	16.9	340	12.7	361	8.5	398
LU26S	7	0.47	486	29.1	342	31.4	384	5.7	435
Punjab-85	8	0.31	581	15.0	435	17.4	443	43.3	512
Pato	9	0.91	716	21.5	400	80.5	432	29.0	574
7-Cerros	5	0.21	605	14.3	267	56.4	385	14.6	495
PAK-81	3	0.28	617	10.4	272	33.2	518	33.6	568
Kharchia-65	7	0.88	623	3.71	285	44.9	474	8.0	549
Site means	7		556		351		430		

LSD at p = 0.05

Na^+ :
Between varieties on normal soil = 2.17 (***)
Between varieties on sodic soil = 71.5 (**)

K^+ :
Between site means = 24.02 (***)
Between variety means = 53.22 (***)
Between variety x site interaction means = 75.26 (**)

sodium contents were noted in SARC-2 and lowest in PAK-81. In the sodic soil, highest sodium concentrations in flag leaves were noted in Punjab-85 (salt sensitive variety) and lowest in 7-Cerros and PAK-81 (moderately salt tolerant varieties). The sodium contents of the two salt tolerant varieties (LU26S and Kharchia-65) was also considerably lower than those of the salt sensitive varieties.

For K^+, there were significant differences between varieties under both normal and sodic soil conditions. Under normal soil conditions, potassium contents of flag leaves were highest in Pato and lowest in SARC-4. In sodic soil, a decrease ranging from 5% (SARC-3) to 39% (Pato) was noted in different varieties. The decrease in potassium content of the salt tolerant varieties LU26S and Kharchia-65 (21% and 24% respectively) was similar to that of the salt sensitive Punjab-85 (24%).

K^+/Na^+ ratios were calculated from the sodium and potassium data shown in Table-4.9 and are presented in Table-4.10. High K^+/Na^+ ratios were found in the flag leaves of different varieties under normal soil conditions which ranged from 54.5 in SARC-2 to 241.3 in PAK-81. Highest K^+/Na^+ ratios were noted in PAK-81 and 7-Cerros both being moderately salt tolerant varieties. These ratios were also quite high in the salt tolerant variety Kharchia-65.

Under sodic conditions there was a marked decrease in K^+/Na^+ ratios in all the varieties. K^+/Na^+ ratios were comparatively higher in the salt tolerant varieties LU26S and Kharchia-65 compared to the salt sensitive variety Punjab-85. A higher ratio was noted in Kharchia-65 than in LU26S although both of these have been reported as salt tolerant.

4.3.7 Grain Weight per spike and Yield Components

Number and weight of grains per main spike and 100 grain weight were significantly decreased under sodic conditions as compared to normal soil (Table - 4.11). In the analysis of variance, the effects of variety and site were highly significant for number of grains, weight of grains and 100 grain weight. Variety x site interaction was significant for number of grains and weight of grains per spike but non-significant for 100 grain weight.

Grain weight of all varieties was decreased under sodic conditions. The decrease was significant in all the varieties except Pato. Number of grains were also decreased as a result of sodic conditions. The decrease was found to be significant in SARC-2, SARC-3, Punjab-85, 7-Cerros, PAK-81 and Kharchia-65. Similarly, 100 grain weight also decreased under sodic soil

Table - 4.10: K^+/Na^+ ratios in flag leaves of different wheat varieties

Varieties	Normal soil		Sodic soil	
	Means	± SE	Means	± SE
SARC-1	80.8	5.80	0.82	0.07
SARC-2	54.5	1.76	1.16	0.31
SARC-3	84.0	5.69	1.58	0.11
SARC-4	50.1	2.39	1.07	0.06
LU26S	68.5	6.34	1.14	0.12
Punjab-85	75.5	4.88	1.03	0.15
Pato	80.9	10.30	1.22	0.36
7-Cerros	118.8	2.18	1.63	0.44
PAK-81	241.3	25.6	2.00	0.38
Kharchia-65	85.9	10.3	1.74	0.25
Site means	94.0		1.30	

LSD between varieties on normal soil = 13.8 (*)
LSD between varieties on sodic soil = 0.92 (*)

Table - 4.11: Grain weight per spike and yield components of main shoots of different wheat varieties

Varieties	Normal soil						Sodic soil					
	Number of grains/spike		Weight of grains (g)		100 grain weight (g)		Number of grains/spike		Weight of grains (g)		100 grain weight (g)	
	Means	± SE	Means	± SE	Means	± SE	Means	± SE	Means	± SE	Means	± SE
SARC-1	38.1	2.15	1.90	0.09	5.05	0.09	29.1	2.02	1.16	0.12	3.73	0.22
SARC-2	51.4	1.73	2.47	0.08	4.83	0.09	35.8	1.71	1.31	0.08	3.63	0.10
SARC-3	53.9	2.01	2.63	0.09	4.91	0.08	38.3	2.65	1.45	0.14	3.56	0.19
SARC-4	40.8	1.77	2.13	0.09	5.23	0.07	36.5	1.60	1.54	0.11	4.11	0.18
LU26S	44.8	2.45	2.37	0.12	5.32	0.05	36.6	1.97	1.57	0.13	4.12	0.20
Punjab-85	55.3	2.17	2.39	0.09	4.34	0.05	42.7	2.15	1.50	0.11	3.40	0.14
Pato	51.1	1.80	1.74	0.06	3.42	0.08	41.0	2.23	1.25	0.09	3.01	0.12
7-Cerros	71.6	2.01	2.86	0.09	3.99	0.04	59.4	1.37	2.11	0.07	3.54	0.06
PAK-81	73.2	2.29	3.51	0.12	4.82	0.10	35.0	1.87	1.37	0.11	3.88	0.22
Kharchia-65	43.0	2.43	1.91	0.12	4.42	0.08	27.0	1.86	1.05	0.08	3.88	0.06
Site means	52.3		2.4		4.6		38.1		1.4		3.7	

Varietal means

	SARC-1	SARC-2	SARC-3	SARC-4	LU26S	Punjab-85	Pato	7-Cerros	PAK-81	Kharchia
No. of grains/ear	33.6	43.6	45.9	38.6	40.7	49.0	46.1	65.5	54.1	35.0
Wt. of grains/ear	1.53	1.89	2.04	1.83	1.97	1.95	1.50	2.49	2.44	1.48
100 Gr. wt (g)	4.39	4.23	4.29	4.67	4.72	3.87	3.21	3.77	4.35	4.15

LSD at p = 0.05

Site means for no. of grains/spike=3.47 (***), weight of grains/spike= 0.19 (***), 100 grain weight = 0.26 (***)

Variety means for no. of grains/ spike=7.70 (***), weight of grains/spike= 0.42 (***), 100 grain weight = 0.57 (***)

Variety x site means for no. of grains/ spike =10.89 (**), weight of grains/spike= 0.59 (*), 100 grain weight = (NS)

All values are means of thirty observations.

conditions and the decrease was significant in all the varieties except Pato, 7-Cerros and Kharchia-65. Under sodic conditions, 7-Cerros had significantly higher mean grain weight per main spike while in the normal soil, PAK-81 produced the significantly highest weight of grains.

Grain and straw yield per square metre (Table-4.12) was too, significantly decreased as a result of stress in all the varieties. The salt tolerant varieties LU26S and 7-Cerros had higher yield than all the other varieties under normal soil conditions, but were statistically similar to SARC-2, SARC-4 and Punjab-85. Under sodic conditions, 7-Cerros gave the greatest yield as compared to other varieties but was significantly similar to all the other varieties except SARC-2. Straw yield (g/m^2) was also high in 7-Cerros in the normal soil and was significantly similar to all the other varieties except SARC-1 and SARC-3. In the sodic soil, straw yield was greatest in PAK-81 but was significantly similar to all the other varieties. In the analysis of variance, the effects of variety, site and the variety x site interaction were highly significant for grain yield (g/m^2). Straw yield was significantly different between sites while varietal differences and the variety x site interaction were non-significant.

4.3.8 Correlation of Results

A main objective of this experiment was to study associations between traits, and in particular to identify traits that might be associated with increased stress tolerance. Values of the coefficient of linear correlation between weight of grains per main spike and all measured traits were calculated separately for normal and sodic soils collectively for all the varieties and are presented in Table 4.13.

In normal soil weight of grains per spike was significantly and positively correlated with length and weight of main spikes, weight of main shoots, number of grains per spike, and K^+/Na^+ ratio. A significant negative correlation was observed between sodium content of flag leaves and grain weight per spike.

In sodic soil significant positive correlations were observed between grain weight per spike and length and weight of main shoots and spikes, number of grains per spike, 100 grain weight, number of total tillers and ears per plant. Correlations between ion contents and grain weight per spike were non-significant. The correlations between grain weight and flag leaf area was not significant under normal as well as sodic soil conditions.

Coefficients of correlations were also calculated for normal and sodic soils separately

Table - 4.12: Grain and straw yield (g/m^2) of different wheat varieties

Varieties	Normal soil				Sodic soil				Variety means	
	Grain		Straw		Grain		Straw		Grains	Straw
	Means	± SE	Means	± SE	Means	± SE	Means	± SE		
SARC-1	403	63	389	82	160	25	137	9	282	263
SARC-2	575	49	547	55	113	16	145	30	344	346
SARC-3	507	82	478	45	125	50	122	13	316	300
SARC-4	570	5	580	20	185	12	168	51	377	374
LU26S	645	54	618	50	223	26	207	19	434	412
Punjab-85	532	41	527	57	149	9	148	22	340	337
Pato	432	60	589	99	125	20	113	19	278	351
7-Cerros	628	63	633	94	235	37	218	53	432	425
PAK-81	345	12	547	72	213	7	257	24	279	401
Kharchia-65	387	22	545	53	195	12	248	10	291	397
Site means	502		545		172		176			

LSD at p = 0.05
Site means for grains/m^2 = 36.2 (***), Straw weight/m^2 = 47.1 (***)
Variety means for grains/m^2 = 80.2 (***), Straw weight /m^2 = (NS)
Variety x site means for weight of grains/m^2 = 113.5 (**), Straw weight/m^2 = (NS)
All values are means of three replications.

Table - 4.13: Linear correlation coefficients between grain yield per main spike and different yield components of different wheat varieties under normal and sodic soil conditions

Parameters	Normal soil	Sodic soil
Flag leaf area (cm^2)	0.213 NS	0.039 NS
Length of main shoots (cm)	0.108 NS	0.721 **
Length of main shoot spikes (cm)	0.548 **	0.637 **
Weight of main shoots (g)	0.885 **	0.886 **
Weight of main shoot spikes (g)	0.993 **	0.991 **
Number of grains per spike	0.885 **	0.872 **
100 grain weight (g)	0.135 NS	0.605 **
Number of total tillers per plant	0.108 NS	0.601 **
Number of ears per plant	0.309 NS	0.522 **
Na^+ contents of flag leaves (μ mol/g dry weight)	-0.575 **	0.052 NS
K^+ contents of flag leaves (μ mol/g dry weight)	0.082 NS	-0.325 NS
K^+/Na^+ ratio in flag leaves	0.674 **	-0.167 NS

- NS= Non-significant at 5% level of significance
- * = Significant at 5% level of significance
- ** = Significant at 1% level of significance

between grain weight per main spike, different gas exchange parameters and sodium and potassium contents of the flag leaves (Table - 4.14) using the data for the four varieties (SARC-1, LU26S, PAK-81 and Kharchia-65) used for determination of gas exchange parameters.

In normal soil weight of grains per main spike was not significantly related to all the gas exchange parameters. A significant positive correlation however was noted between Pn and sodium contents of flag leaves ; and Pn vs. E and g_s. There was a significant negative correlation between Pn and leaf temperature. A high significant positive correlation was also observed between g_s and E. The correlation between Pn and Ci was non-significant. There were no significant correlations between potassium contents, K^+/Na^+ ratio of the flag leaves and Pn .

In sodic soil, significant positive correlations were observed between Pn vs. g_s and E vs. g_s. All other correlations were non-significant.

Non-significant negative correlations existed between potassium contents, K^+/Na^+ ratios of flag leaves, sub-stomatal carbon dioxide (Ci) and grain weight per spike. Correlations between Pn and sodium, potassium and K^+/Na^+ ratios of flag leaves were non-significant.

4.4 DISCUSSION

Experimental site (sodic) in this experiment was a dense non-saline sodic with extremely low porosity and hydraulic conductivity and due to these properties, it is considered to be an unfavourable soil for growing most crops including wheat.

Growth and yield:

Growth and yield are affected by salt stress to varying degrees in different crop plants (Maas and Hoffman, 1977). All the growth parameters were adversely affected under sodic conditions as compared to the normal soil in this study. However, the magnitude of this adverse effect was different in different varieties and parameters.

Percent reduction in the grain yield over control is usually considered as a criterion for salinity or sodicity tolerance (Qadar, 1993). According to this criterion, varieties 7-Cerros, LU26S and SARC-4 suffered least reduction in grain yield (weight of grains per spike) in the sodic soil and proved to be tolerant to sodicity while the varieties Kharchia-65, SARC-1 and Pato were adversely affected and gave the lowest relative yield and proved sensitive to sodicity. Pato has been reported to be a salt sensitive variety by Akhtar *et al.* (1994). A close examination of

Table - 4.14: Linear correlation coefficients between grain yield per main spike and different gas exchange parameters in four wheat varieties under normal and sodic soil conditions

Parameters	Normal soil	Sodic soil
Pn of flag leaves vs. grain yield per main spike	0.344 NS	0.316 NS
g_s of flag leaves vs. grain yield per main spike	0.378 NS	0.080 NS
Evapotranspiration (E) vs. grain yield per main spike	-0.006 NS	0.274 NS
Ci vs. grain yield per main spike	0.098 NS	-0.128 NS
Leaf temperature vs. grain yield per main spike	-0.314 NS	0.517 NS
Pn vs. E	0.593 *	0.758 **
Pn vs. g_s	0.690 *	0.527 NS
Pn vs. Ci	-0.094 NS	-0.026 NS
Pn vs. leaf temperature	-0.655 *	0.404 NS
g_s vs. E	0.819 **	0.907 **
Pn vs. Na^+ contents of flag leaves	0.709 **	0.047 NS
Pn vs. K^+ contents of flag leaves	-0.164 NS	-0.174 NS
Pn vs. K^+/Na^+ in flag leaves	0.467 NS	-0.156 NS

- NS= Non-significant at 5% level of significance
- * = Significant at 5% level of significance
- ** = Significant at 1% level of significance

the growth and yield parameters noted here revealed that all the attributes may not be equally tolerant or sensitive to salinity/sodicity. For example under sodic soil conditions, 100 grain weight was greatest in LU26S and lowest in Pato but weight of grains per spike was greatest in 7-Cerros and lowest in Kharchia-65. It was also noted that a variety which gave high yield under normal soil conditions, did not necessarily gave high yield under sodic soil conditions e.g. variety PAK-81 gave the highest grain yield per spike under normal soil conditions but its yield under sodic conditions was lower than 7-Cerros, LU26S, SARC-4 etc. It was also noted that Punjab-85 which was the most salt-sensitive variety in the greenhouse and saline soil conditions (see Chapters 2 and 3) proved relatively more tolerant to sodicity as compared to the salt-tolerant variety Kharchia-65.

Grain yield (g/m^2) in the sodic soil was also higher in 7-Cerros and LU26S varieties which showed that these are tolerant to sodic conditions while Pato, SARC-1 and Kharchia-65 gave the lowest yield and proved to be sensitive to sodicity. Straw yield was the greatest in PAK-81 and Kharchia-65 under sodic conditions. High straw yield and low grain yield in Kharchia-65 in the sodic soil suggests the presence of some inhibitory mechanism for the process of gas exchange or transport of assimilates to the grains. This can not be explained on the basis of higher salt build up in the plants due to higher transpiration rates (Munns and Termaat, 1986), as the gas exchange measurements were made during the later part of the reproductive phase. By that time sufficient damage might had already occurred in respect of salt accumulation in the leaves which was responsible for nutrient imbalances, early senescence, retarded production or transport of carbohydrates (Munns and Termaat, 1986) to the grains which decreased its yield. Downton, (1977) also reported that the plants exposed to NaCl stress for long periods are likely to have a low carbohydrate status. Munns (1992) reported that chemicals sent from roots in the transpiration stream could control leaf expansion, and that xylem sap from plants in dry or saline soil could contain increased amounts of a growth inhibitor, or decreased amounts of a growth promoter with unknown identity. The effect of this growth inhibitor might have affected Kharchia-65 more than other varieties under dry and dense sodic soil conditions with poor porosity.

Higher yield of 7-Cerros and LU26S seemed to be due to their better flag leaf area, dry weight of main shoots and spikes, comparatively lower sodium accumulation in the leaves and better photosynthetic efficiency under sodic conditions. Better performance of LU26S has been reported under salt stress by other workers (Ashraf and McNeilly, 1991; Qureshi *et al.* 1993) and the results of this study showed that it is comparatively better tolerant to sodic conditions also.

Hollington *et al.* (1992) reported that 7-Cerros gave the highest grain yield under saline conditions as compared to some other varieties. Performance of 7-Cerros under sodic conditions was even better than LU26S and needs attention of the breeders for using this variety in the breeding programmes for evolving varieties for saline-sodic or sodic soils.

There was about 50% decrease in the flag leaf area in all the varieties as a result of stress caused by sodic soil. Leaf area of SARC-2, SARC-1, LU26S and 7-Cerros was comparatively less affected while that of Kharchia-65 was affected the most. This can be contrasted with the findings of greenhouse experiment conducted at the University of Wales, Bangor (see chapter 2, section 2.3.2) where Kharchia-65 was at the top in total leaf area and also the findings of Srivastava *et al.* (1988). This could be the major reason for low yield of Kharchia-65 at this site. Poor performance of Kharchia-65 at this site could be due to highly sodic soil coupled with nearly water stress caused by dense soil conditions with a very low porosity associated with low aeration in the soil. Gill *et al.* (1993) reported that Kharchia-65 though tolerant to sodicity was less tolerant to the combined effect of sodicity and waterlogging.

There seemed to be no effect of tiller length on the grain yield in the normal soil but it was significantly correlated in the sodic soil. Weight of the main shoots, number and weight of main shoot spikes were significantly correlated with the grain yield per spike indicating thereby that wheat varieties which are capable of maintaining spike length and weight under sodicity stress may be expected to exhibit tolerance to sodicity. Gill *et al.* (1992) conducted a field experiment on sodic soil and observed that grain weight and to a lesser extent 100 grain weight was decreased with rise in pH of the soil.

Na^+, K^+ and K^+/Na^+ ratio:

There was a very high and significant increase in Na^+ contents and comparatively less but significant decrease in K^+ contents in the flag leaves of all the varieties. This antagonism of Na^+ with K^+ has also been reported by Epstein (1972) and Gorham (1994). Gorham (1992) reported that salt-tolerant wheat varieties have lower leaf Na^+ concentrations than the salt-sensitive genotypes when grown in solutions containing high concentrations of NaCl. Qadar (1993) reported significant increase in Na^+ and decrease in K^+ contents in the shoots of rice under sodic conditions. The highest yielding variety 7-Cerros accumulated the lowest amount of Na^+ and had quite high K^+/Na^+ ratio in the sodic soil. A high K^+/Na^+ ratio in shoot and better salt tolerance was also reported for wheat and tall wheat grass by Shannon (1978) and Qadar (1993) . However, this did not fully explain the varietal tolerance to sodicity as the second highest yielding variety LU26S accumulated quite high amount of Na^+. Interestingly Na^+ contents in Kharchia-65 were very low and in spite of this, it produced the lowest grains per spike. Distinct varietal differences were also noted for K^+ contents of the flag leaves. PAK-81 had the highest K^+ contents. SARC-1 which was one of the adversely affected varieties had comparatively low K^+ but contrary to this, Kharchia-65 which was also adversely affected had quite high K^+ contents. Genotypic differences in Na^+ uptake rate as well as its cellular tolerance in wheat may cause different patterns of Na^+ accumulation through time (Schachtman and Munns, 1992). The linear correlation coefficients (r) between the weight of grains per spike and Na^+ , K^+ and K^+/Na^+ ratios were also found to be non-significant in the sodic soils (see Table 4.13), which showed that these values can not be used with confidence as an indicator for tolerance against sodicity. Yasin (1991) reported an increase in leaf Na^+ and a decrease in K^+ contents with increasing Na^+ and ESP of the soil. Grain and straw yields were also reported to decrease at an ESP of 38.5 and 56.4 (3.6 and 4.45 dS m^{-1} salinity respectively). Sharma (1991) compared Kharchia-65 (resistant) and HD 4502 (sensitive) wheat varieties in pots at different ESP levels and found that plant Na^+ concentration was greater in the sensitive than in the tolerant variety. At pH 9.4 and 9.6, Na^+ concentration in the leaves of salt-sensitive HD4502 was >2% while in Kharchia-65 (resistant), all leaves had <2% Na^+.

Generally, the varieties with high K^+ contents under normal conditions had also high K^+ contents under sodic conditions, but this was not always true. Pato had the highest K^+ contents in the normal soil but in the sodic soil it was not so high. Similar results were also reported by Qadar (1988) in case of rice.

Gas exchange:

Plant biomass production depends on the ability of the plants to accumulate carbon products during the process of photosynthesis which is a product of rate of photosynthesis per leaf area and the leaf surface available for this purpose. Rates of photosynthesis are usually lower in NaCl treated plants and may decrease with time of exposure to a given NaCl level (Yeo *et al.* 1985; Munns and Termaat, 1986). Prolonged transpiration will cause salts to build up in the leaves. In this experiment, the data showed that sodicity stress had a very detrimental effect on photosynthesis rate as compared to normal soil in all the four varieties. Decrease in Pn was associated with a similar decrease in g_s and a decrease in Ci also. This trend suggests that decrease in Pn was due to partial closing of the stomata rather than non-stomatal factors. There seems to be no relation of Na^+ contents of the flag leaves with the gas exchange rate as the differences in Pn were not similar to the differences in Na^+ contents in different varieties. e.g. In SARC-1 and LU26S, there was a 76 times and 47 times increase in Na^+ contents at the sodic site respectively while corresponding decreases in Pn were 33% and 6%. Similarly, in PAK-81 and Kharchia-65, increases in Na^+ contents at the sodic site were 103 times and 37 times respectively while corresponding decreases in Pn were 30% and 23% only. Slightly low Pn at the normal site suggests the effect of age on Pn because the measurements were taken at advanced grain filling stage and Pn is said to decrease with increasing age and onset of senescence. LU26S was least affected comparatively which may be one of the reasons for its better yield and sodicity tolerance in spite of the fact that its flag leaf area was lower than some varieties. Stomatal conductance (g_s)and transpiration rate (E) were also significantly decreased. The effect of sodicity was found to be minimum in the salt tolerant variety LU26S. Ci was similar in the salt tolerant variety Kharchia-65 and LU26S. These findings are in agreement with those reported by Kalaji and Nalborczyk (1991) in case of barley. Leidi *et al.* (1991), however reported that at a salinity stress of 25-100 mol m^{-3} NaCl under greenhouse conditions, there was no effect on photosynthesis and transpiration but stomatal conductance was decreased. Although Pn and yield in the salt-tolerant variety LU26S suffered less depression due to sodicity, the coefficients of linear correlations (r) calculated for pooled data of four varieties did not show any significant relationship between the grain yield and Pn (see Table - 4.14). In a greenhouse experiment conducted on wheat, Khan (1996) did not report any significant decrease Pn as a result of increasing ESP of the soil.

4.5 CONCLUSIONS

Punjab-85 which was the most salt-sensitive variety in the greenhouse and saline soil conditions proved relatively more tolerant to sodicity and seemed to possess medium tolerance to sodicity which was reflected in comparatively smaller effects on its spike weight and yield components.

7-Cerros and LU26S proved to be tolerant to sodicity due to their ability to maintain higher flag leaf area and dry weight under sodic conditions. Higher rate of gas exchange under sodic conditions might also be a possible reason for its better performance.

Kharchia-65 is a salt-tolerant variety but it did not prove tolerant to sodic conditions due to its failure to maintain proper flag leaf area and dry weight under very dense sodic soil conditions.

The correlations of Na^+, K^+ contents of the flag leaves and K^+/Na^+ ratios with the grain yield were found to be non-significant in the sodic soils, which showed that these values can not be used in isolation as an indicator for screening of wheat varieties for tolerance against sodicity.

CHAPTER 5

EFFECT OF DIFFERENT PHOTOSYNTHETIC PHOTON FLUX DENSITIES ON GAS EXCHANGE OF TWO WHEAT VARIETIES HAVING CONTRASTING SALT-TOLERANCE UNDER SALT STRESS

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5.1 INTRODUCTION

Plant response to different photosynthetic photon flux densities (PPFD) has been the focus of many research workers and has been studied quite extensively (Gauhl, 1976; Patterson *et al.* 1978; Ball and Critchley, 1982; Holt, 1995; Jones *et al.* 1995). Biomass production and yield of crops depends on the capacity of plants to photosynthesize under different environmental conditions. Photosynthesis has been described as a function of as many as 13 different parameters, but PPFD is the most important single major factor which determines its rate (Marshall and Biscoe, 1980a). Light intensities received by different crops on sunny days usually range from 1700-2000 μmol m^{-2} s^{-1} (Sharma and Singh, 1989); and may fall to less than 200 μmol $m^{-2}s^{-1}$ on cloudy days. The rate of photosynthesis may also vary as a result of different stresses and age of the leaf or plants.

Different environmental conditions e.g. low moisture supply to the roots, nitrogen shortage, high temperature and salinity hasten senescence and decrease leaf area duration (Simmons, 1987). The salt stress in wheat increases stomatal and mesophyll resistance which in turn decreases photosynthesis (Kingsbury *et al.* 1984; Rawson, 1986). In contrast to this, Kemal-ur-Rahim (1988) reported that salinity had little effect on photosynthesis in wheat. Iqbal (1992) fitted an exponential model to his gas exchange data to derive Pn_{max} , α (photosynthetic efficiency) and I_c (photon flux compensation point) and reported that Pn_{max} was significantly decreased by salinity on all sampling dates. He also observed that generally salinity had no significant effect on α but I_c was found to be significantly higher at 100 and 200 mol m^{-3} NaCl than at 0 mol m^{-3} NaCl. Rawson (1986) reported that salinity increased leaf chloride contents and reduced peak photosynthesis (Pn_{max}) , the initial slope (α) of the light response curves and dark respiration of young leaves at ligule emergence and also that dark respiration of slightly older leaves was increased by salinity. Reduction in photosynthetic capacity is usually associated with decrease in leaf expansion and growth caused by salinity (Flowers *et al.* 1986; Munns and Termaat, 1986). The excessive accumulation of Na^+ in the leaves causes their premature senescence (Schachtman and Munns, 1992). Yeo *et al.* (1985, 1991) reported that accumulation of NaCl in the leaves caused a rapid reduction in net photosynthesis and growth of rice. Terry and Waldron (1984) reported that salinity decreases stomatal conductance which causes reduction in transpiration and an increase in leaf temperature.

The drop in net photosynthesis is not merely due to an excessive accumulation of Na^+ in the leaves but also due to senescence of the leaves associated with Na^+ build-up with increasing age. The leaves which remain exposed to salinity for longer periods, are bound to accumulate more salts through the transpiration stream and with an increase in transpiration, there is an increase in net transport of Na^+ to the shoot (Yeo and Flowers, 1986). For any given leaf, net photosynthesis reaches its peak soon after the leaf attains its maximum area (Austin *et al.* 1982; Rawson *et al.* 1983; Kemal-ur-Rahim, 1988). In the flag leaf, the rate of photosynthesis increases to a maximum 2-4 weeks after emergence (Austin *et al.* 1982). Then, there is a plateau which is then followed by a linear decline as the leaf ages (Dantuma, 1973) and this depends largely on the rate of leaf senescence. In unstressed leaves, photosynthesis remains at its maximum for about 5-12 days (Rawson *et al.* 1983) but in flag leaves this period of maximum photosynthesis may be for several weeks (Dantuma, 1973; Austin and Edrich, 1975). There is much information on changes in net photosynthesis with increase in leaf age but little is known regarding changes in rate of gas exchange due to leaf age under salt stress (NaCl) in wheat cultivars having contrasting tolerance of salinity stress.

The current experiment was planned to test the following hypothesis.

a. that gas exchange response curves of wheat varieties having variable degrees of salt tolerance will be different under stressed and non-stressed conditions.

b. that accumulation of ions in the leaves with increasing age results in a decrease in net photosynthesis and that this decrease is greater in a salt-sensitive variety than in a salt-tolerant variety.

5.2 MATERIALS AND METHODS

5.2.1 Plant Materials

Two wheat varieties were selected for this experiment i.e. LU26S (salt tolerant) and Punjab-85 (salt sensitive). These were selected in view of their performance under field conditions in Pakistan (Chapters 3 & 4).

5.2.2 Growth Room Conditions

The experiment was conducted at University College of North Wales, College Farm, Aber, Gwynedd, UK in a walk-in growth room. Day/night photoperiod was maintained at 16/8 hours with the help of fluorescent tubes and incandescent bulbs giving a total PPFD of about 250 μmol $m^{-2}s^{-1}$. Day/night temperature of the growth room was maintained at 25/20°C. The relative humidity ranged from 40 - 60%.

5.2.3 Sowing of Seeds and Experimental Design

Seeds of LU26S and Punjab-85 varieties of wheat were germinated on capillary matting placed over a plastic pot full of tap water. The seeds were placed for germination in the walk-in growth room on December 14, 1994. Seeds were covered with a sheet of paper to reduce evaporation. The paper sheets were removed after three days when the seeds started germination. Seedlings were transplanted on December 22, 1994 and fixed in the polystyrene lid with the help of small pieces of foam. Pots were filled with tap water before transplantation of the seedlings. Nutrient solution was given 3 days after transplanting. The experiment was laid out in a completely randomised design with three replications.

5.2.4 Nutrient Solution

The experiment was conducted hydroponically in plastic pots of 10 litre capacity which had expanded polystyrene tops. The pots as well as the lids were painted black on the outside to discourage any fungal growth. Sixteen holes were bored in the polystyrene lids to hold the seedlings. Each pot contained 16 plants of a single variety at a spacing of 4 cm x 4 cm. In total there were 6 pots of each variety i.e. three replicates at two salinity levels.

The hydroponic medium consisted of tap water only during germination and up to three days after transplanting. Afterwards, the tap water was replaced by the nutrient solution. Phostrogen was used as a source of macronutrients and modified Long Ashton nutrient solution (Hewitt, 1966) as a source of micronutrients. The full composition of the nutrient solution is given in Appendix - A. Phostrogen (Corwen, Clwyd, UK) is a blended 10-10-27 NPK fertilizer in powder form (Appendix - B). It was applied at the rate of 5.0 g per 10 litre.

5.2.5 Salt Stress

There were two salinity levels i.e. control (0 mol m^{-3} NaCl added) and 100 mol m^{-3} NaCl. These levels were produced by adding calculated amounts of commercial NaCl to the nutrient solution. Salinity was introduced starting 7 days after transplanting at the rate of 25 mol m^{-3} NaCl per day and was raised up to a level of 100 mol m^{-3} NaCl.

5.2.6 Maintenance of the Experiment

The first change of hydroponic culture solution was made 15 days after transplanting. Subsequently, the nutrient solutions and salt stress were renewed every week up to the final harvest of the experiment. The upper surfaces of the polystyrene tops were washed with tap water at the time of solution change to get rid of accumulated salts. The pots were filled daily with tap water to compensate for the loss of water due to evapotranspiration.

The crop growth was excellent in the growth room and there was no attack of any disease or insects.

5.2.7 Gas Exchange Measurements

5.2.7.1 Gas Exchange Measurement Chamber

Gas exchange measurements were made in a small chamber specially built for this purpose and set up in another walk-in growth room. This chamber was 150 cm high, 90 cm wide and 90 cm deep. It had walls on three sides and one side was kept open to place the plants for making the measurements. The chamber walls were made of polystyrene sheets which were lined internally with aluminium foil to avoid any light dispersion. The roof was a transparent perspex tray. The light source (1000 W mercury vapour light bulb) had a stainless steel cylindrical housing around it to minimise light dispersion and was suspended over the chamber roof. The perspex tray had 4 cm high walls with a water inlet and outlet. Tap water was kept flowing in the tray throughout the duration of the measurements. This was done to avoid rise in the internal temperature of chamber due to heat produced by the light source.

5.2.7.2 Infra Red Gas Analyzer (IRGA)

In the present and following studies, gas exchange of wheat was determined with an open system infrared gas analyzer (IRGA, model LCA-2; The Analytical Development Co. Ltd.;

Hoddesdon, England).

The equipment consisted of an analysing unit, an air pump, a data logger and a leaf chamber (Parkinson leaf chamber (PLC)). The IRGA records the difference between incoming and outgoing CO_2 concentration in the atmospheric air which is continuously being pumped through the leaf chamber at a constant flow rate. The air supply is obtained from well above the crop canopy or from out side the room where measurements are being taken. It is dried by passing it through a column of silica gel before it is allowed to enter into the leaf chamber. With the help of the light and H_2O sensors contained in the leaf chamber and an attached data logger, it is used for non-destructive measurement of gas exchange parameters i.e. leaf temperature (Tl), rate of net photosynthesis (Pn), stomatal conductance (g_s), transpiration rate (E) and internal CO_2 (Ci).

5.2.7.3 Set-up of IRGA

The IRGA was set-up adjacent to the measurement chamber. The leaf chamber was fixed inside the chamber in a retort stand and air 'in' and 'out' connections were made with rubber tubing. The incoming air supply was taken from the open air, outside and above the roof of the growth room. A constant volume flow rate of 400 cm^3 min^{-1} dry air into the cuvette from the volumetric air supply unit was maintained. The IRGA was turned on about half an hour before recording the data for purging the system and stabilization of electrical components. Before recording the readings, atmospheric pressure was noted from an aneroid barometer and this input was fed in the data logger along with other inputs i.e. boundary layer resistance (rb = 0.30), response of IRGA to infinite water concentrations ($E_{MAX} = 2.30$) and air flow rate.

After each reading on a leaf, a set of records consisting of inputs from the key board, inputs from the LCA and calculated variables were stored in the data-logger using an RCA 1802 microprocessor which has eight kilobytes of memory, and which was capable of storing 240 sets of records. The data accumulated during a day's work were later transferred onto 3.5" floppy disk at the University Farm where measurements were taken, using a transfer program written in Qbasic and Quatro Pro. The data were then later transferred to the main frame computer at the University for further analysis.

5.2.7.4 Light Intensities (PPFD)

Gas exchange measurements were made at six photosynthetic photon flux densities (PPFD) starting at approximately 2000 and then at 1500, 1000, 500, 250 and 0 μmol m^{-2} s^{-1}. Different PPFD were obtained by using neutral light filters. The actual PPFD ± SE at the three gas exchange measuring times are given below.

PPFD desired	Recorded PPFD at 30 DAS	Recorded PPFD at 40 DAS	Recorded PPFD at 50 DAS
2000	2017 ± 7.1	2015 ± 11.3	2011 ± 7.3
1500	1514 ± 3.6	1508 ± 5.6	1510 ± 5.1
1000	1041 ± 7.6	1014 ± 4.9	1003 ± 6.5
500	517 ± 4.4	513 ± 3.5	513 ± 4.2
250	253 ± 1.8	252 ± 1.2	253 ± 1.9
0	0	0	0

The plants were allowed to acclimatise under the artificial light for half an hour before starting the readings from each pot. The measurements were made on leaves from four randomly selected plants in each pot.

5.2.7.5 Gas Exchange Measurements

The gas exchange measurements were made on fully expanded, attached and healthy fifth leaves, to reduce interplant variability and compare leaves of similar physiological age. The Parkinson leaf chamber (PLC) suitable for cereals/grasses (leaf chamber model - PLCA) with variable leaf area (max. 10 cm^2) was used in these studies. The leaf area was calculated (leaf width from the centre x length of the chamber) and was fed in to the data logger before starting readings on each leaf. The central portion of the leaf was inserted in the leaf chamber with the adaxial side of the leaf uppermost and held horizontally so as to avoid shading by any of the other leaves and to enable the light to fall on the leaves perpendicularly. Measurements were made at: i. young age (30 days after sowing - 30 DAS); ii. middle age (40 DAS) and iii. old age (50 DAS) to study the effects of leaf age.

On each sampling date the measurements were made in all the pots in one replication by shifting them one after the other to the measuring room from the growth room.

The time required for each measurement after change of PPFD and from the close of the hand held leaf chamber to the display of the final stabilized results on the LCD of the data logger was about 3-4 minutes. After stabilization of the reading, it was recorded in the data logger.

5.2.7.6 Fitting of Curve Using Rectangular Hyperbola Model

To study the effects of PPFD on photosynthetic rate, a rectangular hyperbola model was fitted to the data. This model is the most commonly used model of the response of leaf photosynthesis to photon flux density (Landsberg, 1977; Kemal-ur-Rahim, 1988). It is based on a curvilinear progression consisting of two phases i.e. an initial linear phase of increasing photosynthetic rate with PPFD (I) through the photon flux compensation point (I_c) which is then followed by a progressive decrease in the slope of the curve with increase in PPFD to a plateau, the photon flux saturated assimilation rate P. In its simplest form the rectangular hyperbola can be written as:

$$P = \frac{abI}{a+bI} \qquad (1)$$

Where P is gross photosynthesis, a and b are constants and I is photon flux density. As this equation passes through the origin, it assumes that photosynthesis (P) is equal to gross photosynthesis (Pg). To fit this model to the data collected in this study it was necessary to first convert the values of Pn for each individual leaf recorded by the IRGA to values of Pg by adding the corresponding absolute values of R_d i.e. $Pg = Pn + R_d$.

It was necessary to add the absolute values of R_d as the latter is usually expressed as a negative quantity. This model was used by Monteith (1965) and Austin (1982). Acock *et al.* (1976) also reported that this model gives a good fit to observed experimental data. The linear form of equation (1) can be written as follows.

$$\frac{1}{Pg} = \frac{1}{a} + \frac{1}{bI} \qquad (2)$$

This is the same as a linear regression equation i.e.

$$Y = A + BX \qquad (3)$$

where $A = \dfrac{1}{a}$, $B = \dfrac{1}{b}$,

$Y = \dfrac{1}{Pg}$ $X = \dfrac{1}{I}$

The values of A and B determined by linear regression were then used to calculate a and b, from which Pn_{max}, I_c and α were calculated. The model was fitted to each separate response curve i.e. to all the data points (4 leaves from each treatment) at 30, 40 and 50 DAS.

$$'a' = Pg_{max} \text{ hence } Pn_{max} = Pg_{max} + R_d \qquad (4)$$

(assuming that R_d is expressed as a negative quantity)

'b' = α = photosynthetic efficiency or the initial slope of the Pn-I curve.

The value of I_c (photon flux compensation point) is equal to the value of I at Pn = 0, or the value of I at Pg = R_d. To calculate this the observed value of R_d was substituted for Pg in the following equation.

$$I_c = \frac{(a)\,(Pg)}{(ab) - (Pg\,b)} \qquad (5)$$

This equation can also be written as follows.

$$I_c = \frac{(a)\,(Pg)}{b\,(a - Pg)} \qquad (6)$$

The calculated values of Pn max, α, I_c and original values of R_d were analysed by anova to test the significance of the effects of the variety, salinity and leaf age on these parameters.

5.2.7 Sampling of the Leaves for Ion Analysis and Sap Extraction

After measuring gas exchange, the leaves were harvested and placed in 1.5 cm^3 polypropylene microcentrifuge tubes, labelled and stored in a freezer at -10°C for ion analysis. To extract cell sap the polypropylene tubes containing leaves were frozen in liquid nitrogen for about 20-30 seconds. After freezing, these were then taken out of the liquid nitrogen, thawed and crushed with a blunt ended metal rod. A small hole was made at the base of this tube which was then placed in a second similar tube of the same capacity and centrifuged at 8000 rpm for 5 minutes. The sap collected in the second tube was frozen and was used for ion analysis.

5.2.8 Chemical Analysis

The frozen sap was allowed to thaw and necessary dilutions were made with distilled water. Sodium, potassium, calcium and magnesium contents were determined by atomic absorption spectrophotometer (Pye Unicam Model SP-90) while chlorides were determined with an ion selective electrode (Orion Research Microprocessor Analyzer Model-901).

Sodium and potassium were determined at 589 nm and 766 nm wavelengths respectively. The measurements were made in emission mode. The machine was standardized against known standard solutions prepared from analytical reagent grade NaCl for sodium and KCl for potassium before reading the diluted sap samples.

Calcium and magnesium were determined at 422.7 and 285.2 nm wavelengths respectively using the absorbance mode. A calcium and magnesium combined hollow cathode lamp was used for this purpose.

5.2.9 Statistical Analysis

The gas exchange data obtained from the IRGA and ion data were analysed statistically by analysis of variance and means and standard errors of means (SE) were calculated using Minitab statistical programme (version 10.2). Examples of the anova tables are presented at Appendix 5.1 and 5.2.

Significance levels are indicated in the tables by *, ** and *** for 5%, 1% and 0.1% probability levels, respectively. Non-significant effects are indicated by NS. All 'differences' among means reported to be significant are at 5% level of probability.

Tests were made at the 5% probability level when a significant ' F ' value was obtained for treatment effects and significantly different means were compared by calculating a least significance difference by using the following equation:

$$LSD = ((2*EMS)/n)^{1/2})*t_{df}$$

n = Number of observations to calculate a mean

t = Tabulated t value at error degrees of freedom

5.3 RESULTS

5.3.1 Gas Exchange Parameters

In the analysis of variance, the effects of light were significant for almost all gas exchange parameters at all three sampling dates except g_s which was non-significant at all the three leaf ages. There were very few significant interactions also for variety x PPFD and salinity x PPFD. The effects of salinity were generally significant at 30 and 40 DAS but not at 50 DAS. Effects of variety were generally significant at all sampling dates. Variety x salinity interaction was also found to be significant for most of the parameters at different sampling dates. Table 5.1 summarises the significance levels of the main effects and their interactions

5.3.2.1 Changes in Gas Exchange Parameters with Light Intensity

Figures 5.1 to 5.4 show the changes in different gas exchange parameters at different PPFD. As PPFD decreased, there was a progressive decrease in Pn , g_s and leaf temperature while a progressive increase in Ci was noted. In the cases of Pn and Ci differences between treatments were greatest at the highest light intensity. In the cases of g_s and Tl differences were broadly similar at all light intensities.

5.3.2.2 Effect of Salt Stress and Varietal Differences in Gas Exchange Parameters

Salt stress decreased Pn significantly at 30 and 40 DAS (Fig 5.1a, b). At 50 DAS however, the effect of salinity was non-significant (Fig 5.1c). There was no significant difference in between the two varieties at 30 DAS but Pn was significantly higher in LU26S at 40 DAS and 50 DAS.

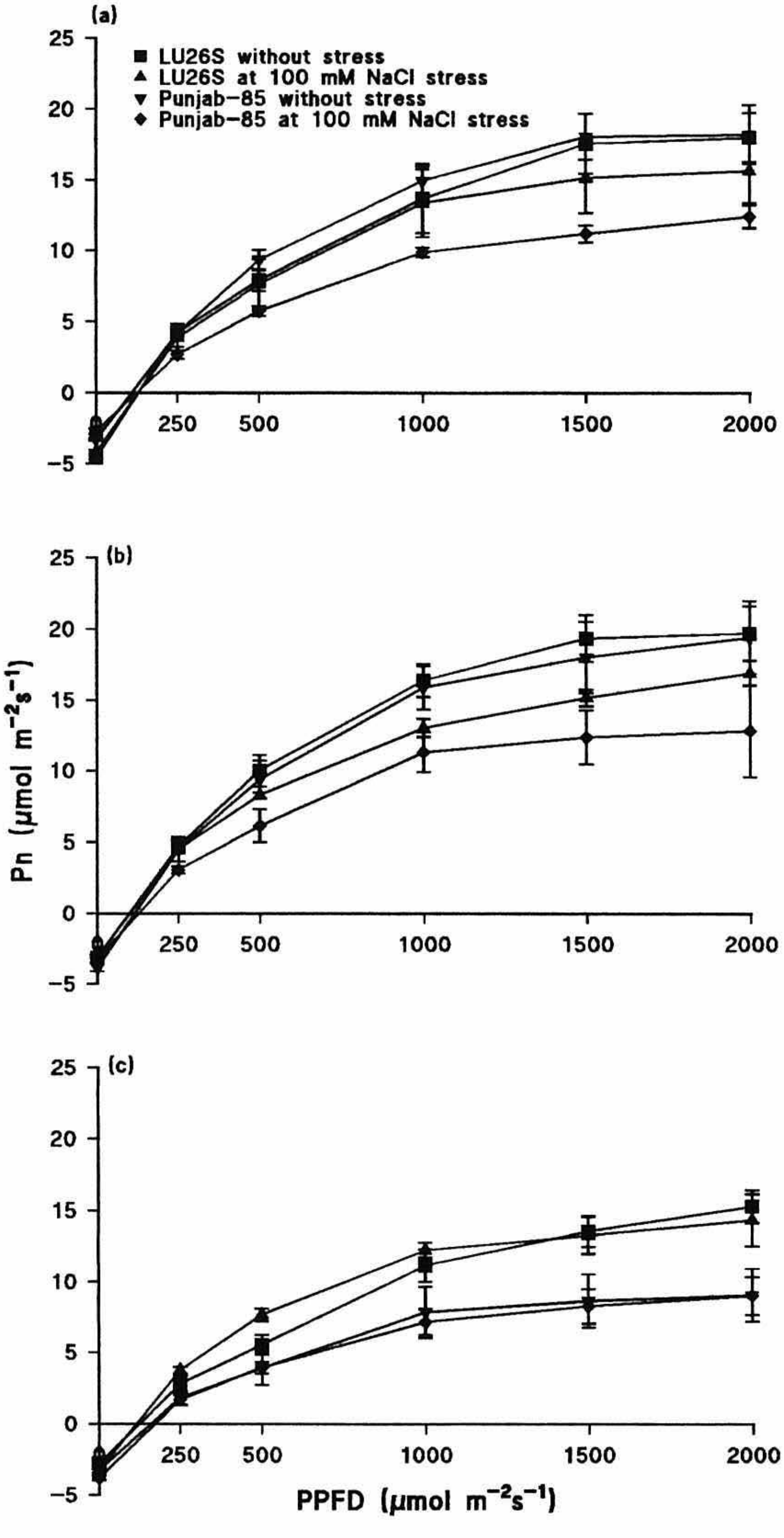

Fig 5.1: Effect of different photosynthetic photon flux densities on net photosynthesis (Pn) at [a] 30 DAS, [b] 40 DAS and [c] 50 DAS in 5th leaves of two wheat varieties.

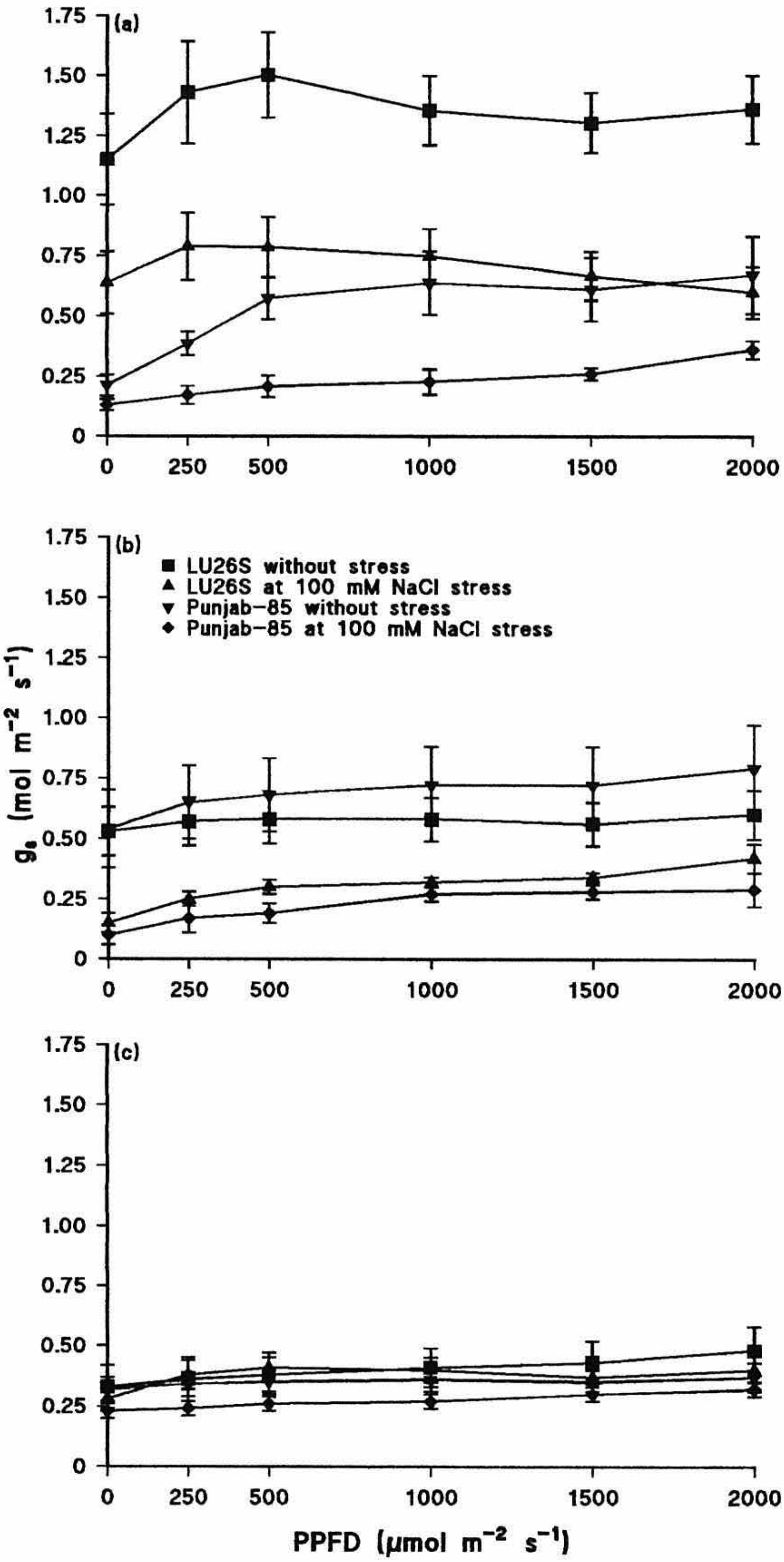

Fig 5.2: Effect of different photosynthetic photon flux densities on stomatal conductance (g_s) at [a] 30 DAS, [b] 40 DAS and [c] 50 DAS in 5th leaves of two wheat varieties.

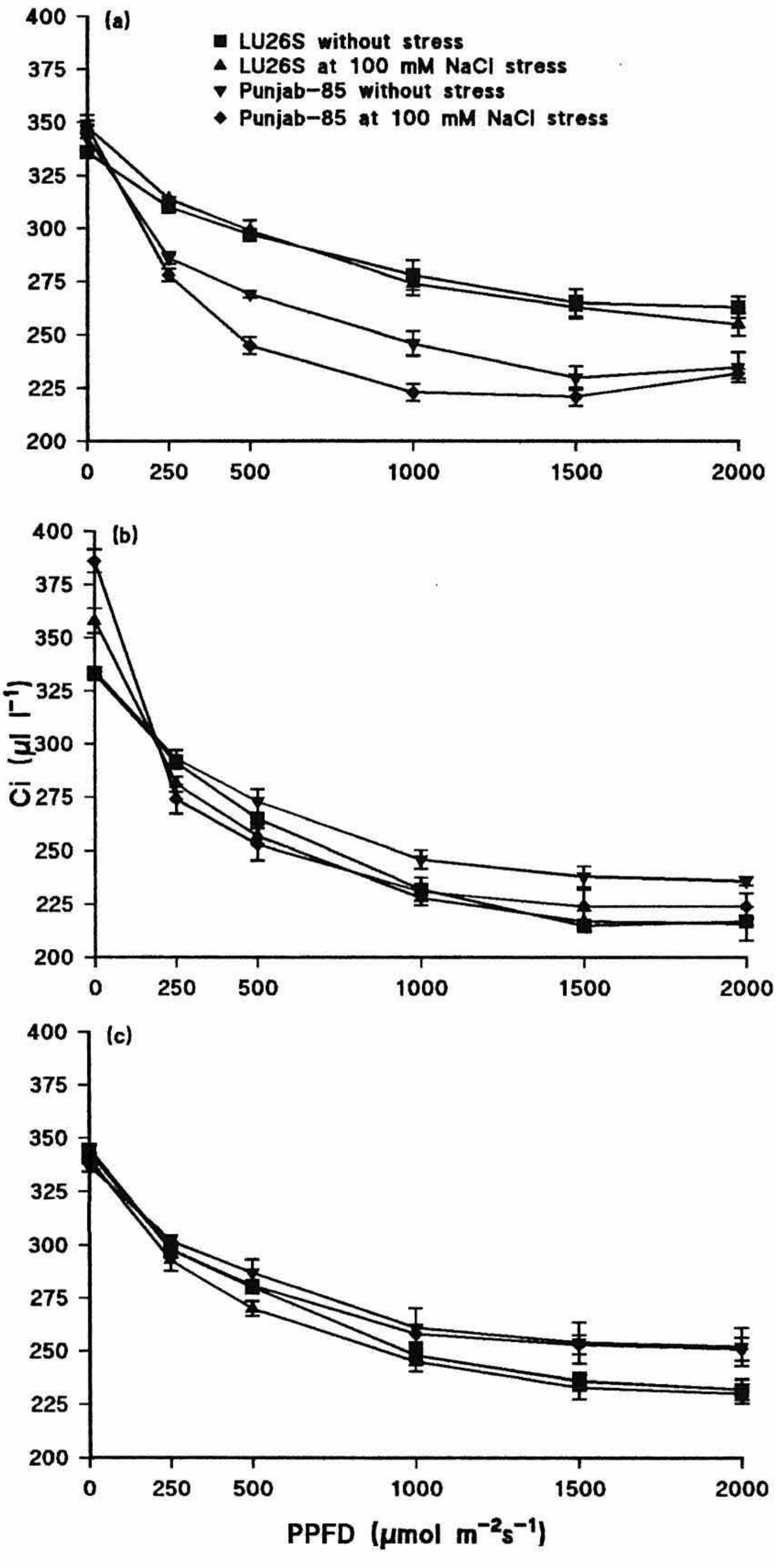

Fig 5.3: Effect of different photosynthetic photon flux densities on sub-stomatal CO_2 (Ci) at [a] 30 DAS, [b] 40 DAS and [c] 50 DAS in 5th leaves of two wheat varieties.

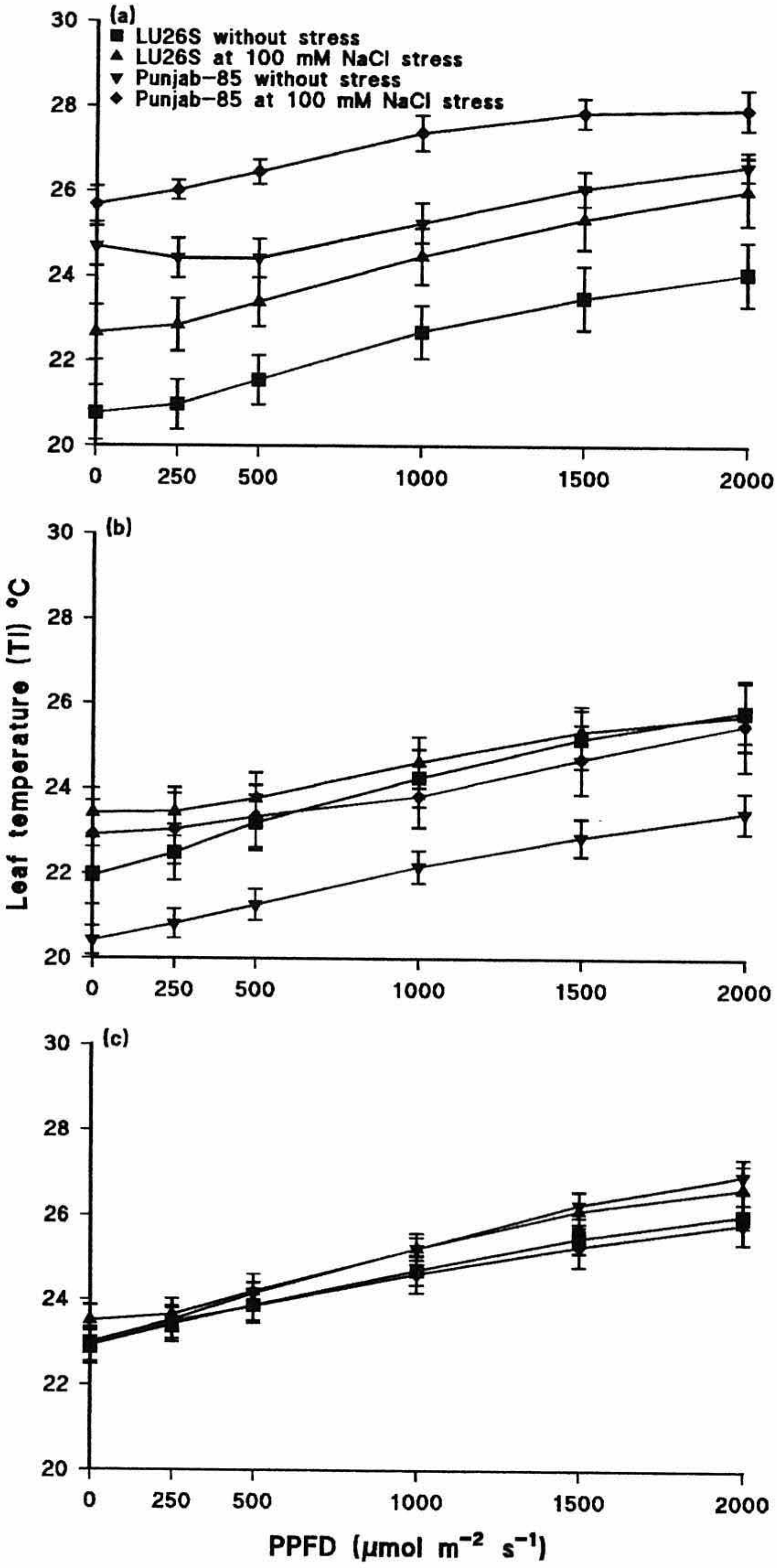

Fig 5.4: Effect of different photosynthetic photon flux densities on leaf temperature (Tl) at [a] 30 DAS, [b] 40 DAS and [c] 50 DAS in 5th leaves of two wheat varieties.

Table - 5.1: Significance levels calculated by analysis of variance for net photosynthesis (Pn, μmol CO_2 $m^{-2}s^{-1}$), stomatal conductance (g_s, mol $m^{-2}s^{-1}$), sub-stomatal CO_2 (Ci, μl l^{-1}) and leaf temperature (°C) at three leaf ages (30, 40 and 50 DAS) in fifth leaves in LU26S and Punjab-85 wheat cultivars at different photosynthetic photon flux densities

Parameters	Variety	Salinity	I	V x S	V x I	S x I	V x S x I
30 DAS							
Pn	NS	***	***	**	NS	NS	NS
g_s	***	***	NS	***	NS	NS	NS
E	***	***	***	**	**	NS	NS
Ci	***	NS	***	NS	**	NS	NS
Leaf temperature	***	***	***	NS	NS	NS	NS
40 DAS							
Pn	*	***	***	NS	NS	NS	NS
g_s	NS	***	NS	*	NS	NS	NS
E	NS	***	***	**	NS	NS	NS
Ci	***	NS	***	NS	NS	***	NS
Leaf temperature	***	***	***	**	NS	NS	NS
50 DAS							
Pn	***	NS	***	***	**	NS	NS
g_s	**	*	NS	NS	NS	NS	NS
E	*	NS	***	**	NS	NS	NS
Ci	***	NS	***	NS	*	NS	NS
Leaf temperature	NS	NS	***	**	NS	NS	NS

- I = Photosynthetic photon flux density
- S= Salinity, V= Variety

* = Significant at 5% probability level
** = Significant at 1% probability level
*** = Significant at 0.1% probability level
NS = Non-significant

g_s was significantly reduced by 100 mol m^{-3} NaCl stress at all sampling dates (Fig 5.2a, b,c). The effects of salinity on E (data not presented) were similar to effects on g_s except at 50 DAS where it was not significantly affected. Significantly higher g_s and E were observed in LU26S at 30 and 40 DAS but at 50 DAS the difference between varieties was non-significant.

Ci was higher at 100 mol m^{-3} NaCl stress at all the leaf ages but this effect was not significant (Fig 5.3a, b, c). Ci was significantly higher in Punjab-85 as compared to LU26S at 30, 40 and 50 DAS.

Leaf temperature (Tl) increased significantly as a result of 100 mol m^{-3} NaCl stress (Fig 5.4a, b) at 30 and 40 DAS but the effect was non-significant at 50 DAS (Fig 5.4c). In Punjab-85 the leaf temperature was significantly higher than in LU26S at 30 and 40 DAS but at 50 DAS the differences were non-significant.

5.3.2.3 Effect of Leaf Age on Gas Exchange Parameters

Taking the gas exchange parameters recorded at the three growth stages together (30, 40 and 50 DAS), it was found that Pn was slightly higher at 40 DAS than at 30 DAS. At 50 DAS, Pn decreased to lower values. The effects of leaf age on Ci and leaf temperature were smaller and the reverse of that observed in Pn i.e. they were lowest at 40 DAS. Highest g_s was recorded at 30 DAS and with age, it decreased. The differences between treatments decreased overtime for g_s and Ci.

5.3.2.4 Effect of Salt Stress and Variety on Observed Values of Pn, g_s, Tl and Ci at the Highest Light Intensity

A separate analysis of variance was conducted for gas exchange data recorded at the highest PPFD. Table 5.2 shows the effects of variety and salt stress on different gas exchange parameters at the highest PPFD (μmol m^{-2} s^{-1}) at 30 DAS (2017±7.1), 40 DAS (2015±11.3) and 50 DAS (2011±7.3) and the levels of significance of the effects of variety, salinity and variety x salinity interaction. Values for the highest PPFD have been presented separately because these were the first values after enclosing the leaf in the leaf chamber before any possible adverse effects on the physiology of the leaf due to the enclosure process. Another reason for using this was that the differences in observed Pn values between the treatments were greatest at the highest light

Table - 5.2: Effect of salinity and variety on net photosynthesis (Pn, μmol CO_2 m^{-2} s^{-1}), stomatal conductance (g_s, mol $m^{-2}s^{-1}$), sub-stomatal CO_2 (Ci, μl l^{-1}) and leaf temperature (°C) at three leaf ages (30, 40 and 50 DAS) in fifth leaves in LU26S and Punjab-85 wheat cultivars at a PPFD (μmol m^{-2} s^{-1}) of 2017±7.1 (30 DAS), 2015±11.3 (40 DAS) and 2011±7.3 (50 DAS).

Leaf age (Days after sowing)	LU26S				Punjab-85				Varietal means	
	0 mol m^{-3}		100 mol m^{-3}		0 mol m^{-3}		100 mol m^{-3}			
	Means	± SE	Means	± SE	Means	± SE	Means	± SE	LU26S	Punj-85
Pn										
30 DAS	18.0	1.74	15.6	2.53	18.2	2.06	12.4	0.81	16.8	15.3
40 DAS	19.7	1.93	16.9	0.91	19.4	2.55	12.8	3.26	18.3	16.1
50 DAS	15.3	1.13	14.3	1.18	9.8	1.56	9.0	1.34	14.8	9.4
g_s										
30 DAS	1.36	0.14	0.60	0.11	0.67	0.12	0.36	0.04	0.98	0.52
40 DAS	0.60	0.10	0.42	0.06	0.79	0.19	0.30	0.07	0.51	0.54
50 DAS	0.48	0.06	0.40	0.08	0.37	0.06	0.30	0.03	0.44	0.34
Ci										
30 DAS	263	4.98	255	5.29	235	7.01	232	2.18	259	234
40 DAS	217	1.78	216	7.85	236	1.81	224	6.22	216	230
50 DAS	232	4.84	230	4.61	252	8.88	252	5.44	231	252
Leaf temperature										
30 DAS	24.1	0.82	26.0	0.80	26.6	0.34	27.9	0.47	25.1	27.3
40 DAS	25.8	0.70	25.7	0.80	23.5	0.48	25.5	1.07	25.8	24.5
50 DAS	26.0	0.28	26.7	0.55	26.9	0.40	25.8	0.48	26.3	26.4

Salinity means

	Pn		g_s		Ci		Tl	
Salinity →	0	100	0	100	0	100	0	100
30 DAS	18.1	14.0	1.01	0.48	250	243	25.3	27.0
40 DAS	19.6	14.9	0.69	0.36	226	220	24.6	25.6
50 DAS	12.6	11.7	0.42	0.36	242	241	26.5	26.2

Level of significance in anova and LSD at $p = 0.05$

Leaf age	Pn			g_s			Ci			Tl		
	V	S	V*S	V	S	V*S	V	S	V*S	V	S	V*S
30 DAS	NS	4.12*	NS	0.26**	0.26**	NS	11.3***	NS	NS	1.41**	1.41*	NS
40 DAS	NS	NS	NS	NS	0.25*	NS	11.2*	NS	NS	NS	NS	NS
50 DAS	3.22**	NS	NS	NS	NS	NS	13.5**	NS	NS	NS	NS	NS

intensities (Fig 5.1a, b, c). Pn was decreased by salinity at all the leaf ages but the effect was significant only at 30 DAS. LU26S had significantly higher Pn than Punjab-85 at 50 DAS. The variety x salinity interaction was not significant for any parameter at any sampling date.

g_s decreased as a result of salinity at all the leaf ages in both the varieties but the effect was significant only at 30 and 40 DAS. g_s also decreased with increase in leaf age in LU26S at 0 and 100 mol m^{-3} NaCl, but this decrease was comparatively smaller in Punjab-85. In Punjab-85 g_s was higher at 40 DAS than at 30 or 50 DAS at 0 mol m^{-3} NaCl stress but at 100 mol m^{-3} NaCl stress, g_s was similar at all leaf ages showing that this was affected even before 30 DAS. LU26S showed significantly higher g_s than Punjab-85 at 30 DAS. Data for transpiration rate are not presented but its trends were nearly the same as were observed for g_s.

Salinity had little effect on Ci at all the leaf ages. Ci was significantly higher in LU26S than in Punjab-85 at 30 DAS but significantly lower at 40 DAS and 50 DAS. Tl was significantly increased by 100 mol m^{-3} NaCl stress at 30 DAS only. LU26S had significantly lower Tl than Punjab-85 at 30 DAS. At other leaf ages, the effects of variety and salinity were non-significant.

5.3.2.5 Effect of Salt Stress and Variety on Calculated Pn_{max}, α, I_c and Observed R_d

The values calculated by the rectangular hyperbola model for Pn_{max}, α, I_c (section 5.2.7.7) and observed R_d values are presented in Table 5.3. In the ANOVA for these parameters the variety x salinity interaction was non-significant at all the sampling dates.

The linear regression equation (equations 2 & 3) provided a significant fit to the data. Values of 'r^2' varied between 90% and 99.8% at 30 DAS, between 90% and 99.9% at 40 DAS and between 90% and 100% at 50 DAS and in all cases these were significant at $p = 0.05$.

Pn_{max}

Pn_{max} was highest at 40 DAS and was lowest at 50 DAS as compared to other sampling dates, which can be due to senescence of the leaves due to their age. In the absence of salt stress, Pn_{max} was higher in Punjab-85 than in LU26S at 30 DAS but it was higher in LU26S at 40 and 50 DAS. At 100 mol m^{-3} NaCl stress, LU26S had higher Pn_{max} at all the three leaf ages but the differences were significant only at 30 and 40 DAS.

The values of Pn_{max} calculated by the rectangular hyperbola model were considerably higher than the actual Pn values observed at the highest light intensity at all the dates at which gas exchange data was recorded (Table 5.2). The differences between fitted and actual values ranged from 4.1 and 11.4 at 30 DAS, from 5.6 and 13.3 at 40 DAS and from 3.2 and 9.5 at 50 DAS (Table 5.4). The trends in treatment effects however, remained nearly the same.

Photosynthetic Efficiency (α)

α was decreased by salt stress at 30 and 40 DAS but the differences were non-significant, but significantly increased by salinity at 50 DAS as compared to control. At both the salinity levels, α was lower at 50 DAS than that at 30 and 40 DAS. Also α was lower in Punjab-85 than in LU26S at all the sampling dates but the differences were significant only at 30 DAS. Comparing figures 5.1a, b and c with the tabulated values (Table - 5.3) showed that the observed values of α were close to the calculated values.

Photon Flux Compensation Point (I_c)

I_c was significantly greater in Punjab-85 than in LU26S at 40 DAS and 50 DAS. At 30 DAS the differences were non-significant. There was no significant effect of salt stress on I_c. Observed values of I_c (figures 5.1a, b and c) were found to be very close to the tabulated values of I_c (Table - 5.3).

Dark Respiration (R_d)

R_d was significantly greater in LU26S than in Punjab-85 at 30 DAS but was significantly higher in Punjab-85 than in LU26S at 40 DAS and 50 DAS. A decrease in R_d due to 100 mol m^{-3} NaCl stress was observed at 30 and 40 DAS but the effect was significant only at 30 DAS. At 50 DAS, R_d was significantly increased by 100 mol m^{-3} NaCl as compared to 0 mol m^{-3} NaCl.

This analysis shows that under salt stress, overall photosynthetic productivity was higher in LU26S than in Punjab-85 due to higher Pn_{max}, higher α, lower I_c and lower observed R_d, particularly at 40 and 50 DAS.

5.3.3 Ion Uptake

Ion analysis was conducted on the cell sap obtained from the same leaf (5th leaf) on which Pn measurements were made. Data for different parameters and leaf ages is presented in Table 5.5 - 5.7.

Table - 5.3: Effect of salinity and variety on calculated maximum photosynthesis (Pn_{max} in μmol $m^{-2}s^{-1}$), photosynthetic efficiency (α in mol CO_2 fixed $m^{-2}s^{-1}$ per mol $m^{-2}s^{-1}$ PPFD), photon flux compensation point (I_c in μmol $m^{-2}s^{-1}$) and observed dark respiration rate (R_d in μmol $m^{-2}s^{-1}$) at three leaf ages (30, 40 and 50 DAS) in fifth leaves in LU26S and Punjab-85 wheat cultivars.

Leaf age (Days after sowing)	LU26S				Punjab-85				Varietal means	
	0 mol m^{-3}		100 mol m^{-3}		0 mol m^{-3}		100 mol m^{-3}			
	Means	± SE	Means	± SE	Means	± SE	Means	± SE	LU26S	Punj-85
Pn_{max}										
30 DAS	26.3	5.6	22.3	4.4	29.6	4.0	16.5	1.2	24.3	23.0
40 DAS	33.0	5.5	22.5	1.3	29.8	4.9	21.0	4.3	27.8	25.4
50 DAS	24.8	3.6	20.3	2.3	13.0	3.3	12.4	2.6	22.6	12.7
α										
30 DAS	0.053	.008	0.047	.003	0.039	.001	0.030	.003	0.050	0.035
40 DAS	0.041	.003	0.042	.001	0.046	.007	0.035	.001	0.042	0.040
50 DAS	0.028	.004	0.041	.003	0.029	.003	0.034	.004	0.034	0.032
I_c										
30 DAS	109.1	13.3	112.0	12.9	92.8	3.3	106.5	6.9	110.5	99.7
40 DAS	85.1	5.1	81.0	2.1	100.0	10.9	110.2	6.3	83.1	105.0
50 DAS	116.9	11.3	93.5	4.4	147.3	18.4	152.7	13.2	105.2	150.1
R_d										
30 DAS	- 4.57	0.09	- 4.16	0.12	- 3.28	0.09	- 2.70	0.19	- 4.37	- 2.99
40 DAS	- 3.12	0.05	- 3.05	0.12	- 3.84	0.27	- 3.25	0.24	- 3.09	-3.55
50 DAS	- 2.77	0.09	- 3.26	0.21	- 3.25	0.18	- 3.82	0.16	- 3.02	- 3.53

Salinity means

	Pn_{max}		α		I_c		R_d	
Salinity →	0	100	0	100	0	100	0	100
30 DAS	28.0	19.4	0.046	0.038	100.9	109.2	- 3.92	- 3.43
40 DAS	31.4	21.8	0.043	0.039	92.6	95.5	- 3.48	- 3.15
50 DAS	18.9	16.4	0.028	0.037	132.1	123.1	- 3.01	- 3.54

Level of significance in anova and LSD at p = 0.05

Leaf age	Pn_{max}			α			I_c			R_d		
	V	S	V*S	V	S	V*S	V	S	V*S	V	S	V*S
30 DAS	NS	NS	NS	0.01**	NS	NS	NS	NS	NS	0.28***	0.28**	NS
40 DAS	NS	9.43*	NS	NS	NS	NS	14.9**	NS	NS	0.42*	NS	NS
50 DAS	6.54*	NS	NS	NS	0.01*	NS	28.1**	NS	NS	0.36*	0.36*	NS

Table - 5.4: Effect of salt stress and variety on differences between calculated Pn_{max} and recorded net photosynthesis ($\mu mol\ m^{-2}\ s^{-1}$) in LU26S and Punjab-85 wheat varieties (+ = increase, - decrease) at a PPFD ($\mu mol\ m^{-2}\ s^{-1}$) of 2017±7.1 (30 DAS), 2015±11.3 (40 DAS) and 2011±7.3 (50 DAS)

Leaf age	LU26S		Punjab-85	
	0 mol m^{-3} NaCl	100 mol m^{-3} NaCl	0 mol m^{-3} NaCl	100 mol m^{-3} NaCl
30 DAS	+ 8.3	+ 6.7	+ 11.4	+ 4.1
40 DAS	+ 13.3	+ 5.6	+ 10.4	+ 8.2
50 DAS	+ 9.5	+ 6.0	+ 3.2	+ 3.2

5.3.3.1 Effect of Age of Leaves and Salinity on Ion contents

Potassium:

At all the three leaf ages (30, 40 and 50 DAS), K^+ was slightly higher in Punjab-85 than in LU26S at both the stress levels (Table 5.5). Differences were significant at 30 DAS and 50 DAS. At 30 DAS salinity resulted in a significant increase in K^+ content in Punjab-85 but not in LU26S. At 40 and 50 DAS, K^+ contents were higher at 100 than at 0 mol m^{-3} NaCl in both varieties. The variety x salinity interaction was only significant at 30 DAS.

Sodium:

Na^+ contents of leaves were significantly higher at 100 than at 0 mol m^{-3} NaCl in both varieties at all the three leaf ages (Table 5.5). At 0 mol m^{-3} NaCl, Na^+ in leaf sap did not change with leaf age. At 100 mol m^{-3} NaCl it increased, the increase being greater in Punjab-85 than in LU26S.

Differences between varieties were non-significant at 30 and 40 DAS but highly significant at 50 DAS. The effect of salt stress was highly significant at all leaf ages. The variety x salinity interaction was significant at 30 and 50 DAS only.

Calcium:

At 0 mol m^{-3} NaCl stress, Ca^{2+} contents were higher in the salt tolerant variety LU26S than in the salt sensitive variety Punjab-85 at 40 and 50 DAS (Table 5.6). Ca^{2+} contents were higher at 40 and 50 DAS than at 30 DAS in both the varieties at 0 mol m^{-3} NaCl.

Salinity decreased Ca^{2+} contents in the leaf sap in both varieties. The decrease was significant in both varieties at 40 DAS, and in LU26S only at 50 DAS.

Magnesium:

In general, at 0 mol m^{-3} NaCl, Mg^{2+} increased with leaf age in both varieties (Table 5.6) but at 100 mol m^{-3} NaCl it decreased. Salinity significantly decreased Mg^{2+} at all the sampling dates. Mg^{2+} was significantly higher in LU26S than in Punjab-85 at all the three leaf ages. The variety x salinity interaction was significant at 30 DAS and 50 DAS.

Table - 5.5: Effect of salinity (100 mol m^{-3} NaCl) and variety on K^+ and Na^+ contents of 5th leaf in LU26S and Punjab-85 wheat cultivars.

Leaf age (Days after sowing)	LU26S				Punjab-85				Varietal means	
	0 mol m^{-3}		100 mol m^{-3}		0 mol m^{-3}		100 mol m^{-3}			
	Means	± SE	Means	± SE	Means	± SE	Means	± SE	LU26S	Punj-85
K^+										
30 DAS	228	8.4	223	9.9	238	5.9	316	23.0	226	278
40 DAS	285	15.6	369	9.9	296	15.6	410	27.3	327	353
50 DAS	265	15.6	348	15.5	280	10.4	410	19.7	306	345
Na^+										
30 DAS	15.2	0.9	27.3	2.6	12.0	0.6	29.9	2.0	21.5	21.0
40 DAS	11.5	2.0	35.1	1.7	11.2	2.6	35.7	1.7	23.3	22.4
50 DAS	13.2	2.8	42.5	5.1	15.8	2.6	78.9	7.8	27.9	47.4

Salinity means

	K^+		Na^+	
Salinity →	0 mol m^{-3}	100 mol m^{-3}	0 mol m^{-3}	100 mol m^{-3}
30 DAS	233.6	269.9	13.9	30.1
40 DAS	290.7	389.3	11.3	34.4
50 DAS	272.5	378.9	14.5	60.7

LSD at p=0.05

Leaf age	K^+			Na^+		
	Variety	Salinity	V*S	Variety	Salinity	V*S
30 DAS	31.35 **	31.35 *	41.81 *	NS	3.28 ***	4.37 *
40 DAS	NS	42.11 ***	NS	NS	4.77 ***	NS
50 DAS	36.14 *	36.14 ***	NS	11.57 **	11.57 ***	15.44 **

Table - 5.6: Effect of salinity and variety on Ca^{2+} and Mg^{2+} contents of 5th leaf in LU26S and Punjab-85 wheat cultivars.

Leaf age (Days after sowing)	LU26S				Punjab-85				Varietal means	
	0 mol m^{-3}		100 mol m^{-3}		0 mol m^{-3}		100 mol m^{-3}			
	Means	± SE	Means	± SE	Means	± SE	Means	± SE	LU26S	Punj-85
Ca^{2+}										
30 DAS	1.8	0.1	1.4	0.1	1.9	0.3	1.8	0.2	1.6	1.9
40 DAS	3.7	0.6	1.1	0.1	3.1	0.6	1.6	0.2	2.4	2.3
50 DAS	3.9	0.2	1.0	0.1	2.1	0.3	1.5	0.1	2.4	2.0
Mg^{2+}										
30 DAS	6.3	0.1	4.1	0.2	4.7	0.2	3.4	0.1	5.2	4.1
40 DAS	6.3	0.3	3.8	0.1	5.6	0.4	3.1	0.2	5.0	4.3
50 DAS	8.8	0.3	2.8	0.3	6.1	0.6	3.1	0.2	5.8	4.6
Salinity means										
	Ca^{2+}				Mg^{2+}					
Salinity →	0 mol m^{-3}		100 mol m^{-3}		0 mol m^{-3}		100 mol m^{-3}			
30 DAS	1.9		1.6		5.5		3.8			
40 DAS	3.4		1.4		5.9		3.5			
50 DAS	3.0		1.4		7.4		2.9			

LSD at p=0.05

Leaf age	Ca^{2+}			Mg^{2+}		
	Variety	Salinity	V*S	Variety	Salinity	V*S
30 DAS	NS	NS	NS	0.43 ***	0.43 ***	0.57 *
40 DAS	NS	1.04 ***	NS	0.69 *	0.69 ***	NS
50 DAS	0.47 *	0.47 ***	0.63 ***	0.91 *	0.91 ***	1.22 **

Chlorides:

Cl^- contents of leaves were significantly greater at 100 than at 0 mol m^{-3} NaCl in both varieties at all the three leaf ages (Table 5.7). At 0 mol m^{-3} NaCl, Cl^- decreased with leaf age but at 100 mol m^{-3} NaCl there was an increase. Differences in Cl^- contents between varieties were not significant at 30 and 40 DAS. At 50 DAS, Cl^- was significantly higher in Punjab-85 than LU26S. At 30 DAS, difference was significant in Punjab-85 but not in LU26S. The variety x salinity interaction was significant at 30 DAS and 50 DAS.

K^+/Na^+:

K^+/Na^+ ratio (Table 5.7) was significantly decreased as a result of salinity in both the varieties at all the three leaf ages. K^+/Na^+ ratio was significantly higher in Punjab-85 than in LU26S at 30 DAS. The differences were non-significant at 40 and 50 DAS. The variety x salinity interaction was non-significant.

5.4 DISCUSSION

Photosynthesis and gas exchange of leaves are affected by many stresses including drought, flooding, salinity, chilling, high temperature, soil compaction and inadequate nutrition. Stomatal conductance and the rate of assimilation of CO_2 per unit leaf area often decreases when stress occurs (Farquhar *et al.* 1989). There are three most important factors which affect the rate of assimilation in crops i.e. CO_2, light and temperature out of which light is the most important cause (Marshall and Biscoe, 1980a). Effects of different light intensities (PPFD) on different gas exchange parameters are discussed in the following paragraphs.

Gas Exchange in response to Different PPFD:

There was a progressive increase in Pn, E, Tl and a decrease in Ci with an increase in PPFD from 0 to 2000 μmol m^{-2} s^{-1}. Higher Pn values were recorded at 30 and 40 DAS than 50 DAS possibly due to a decrease in g_s in the older leaves. Differences in Pn were small at low PPFD values and became greater with increase in PPFD which seemed to be due to similar changes in g_s. LU26S had higher Pn under NaCl stress than Punjab-85. g_s was highest at 30 DAS when there were large differences in between the varieties which decreased with leaf age. Tl (leaf temperature) increased with increase in PPFD. This was due to the direct heating effect of

Table - 5.7: Effect of salinity and variety on Cl^- contents and K^+/Na^+ ratio of 5th leaf in LU26S and Punjab-85 wheat cultivars.

Leaf age (Days after sowing)	LU26S				Punjab-85				Varietal means	
	0 mol m^{-3}		100 mol m^{-3}		0 mol m^{-3}		100 mol m^{-3}			
	Means	± SE	Means	± SE	Means	± SE	Means	± SE	LU26S	Punj-85
Cl^-										
30 DAS	60.5	9.9	83.1	7.9	56.8	2.9	141.0	22.0	71.8	98.9
40 DAS	54.7	5.1	166.7	6.3	55.6	3.9	228.8	27.7	110.8	142.2
50 DAS	37.8	4.9	161.5	19.5	28.6	2.0	260.5	21.8	99.6	144.5
K^+/Na^+										
30 DAS	14.8	1.4	8.3	0.4	20.0	1.3	10.6	0.7	11.5	15.3
40 DAS	27.0	4.4	10.6	0.7	29.7	5.1	12.3	1.1	18.8	21.0
50 DAS	22.0	3.4	8.5	0.9	19.5	3.7	5.4	0.6	15.3	12.4
Salinity means										
Salinity →	Cl^-				K^+/Na^+					
	0 mol m^{-3}		100 mol m^{-3}		0 mol m^{-3}		100 mol m^{-3}			
30 DAS	58.7		112.1		17.4		9.4			
40 DAS	55.2		197.8		28.4		11.5			
50 DAS	33.2		211.0		20.8		6.9			

LSD at p=0.05

Leaf age	Cl^-			K^+/Na^+		
	Variety	Salinity	V*S	Variety	Salinity	V*S
30 DAS	NS	29.52 **	39.38 *	2.34 **	2.34 ***	NS
40 DAS	NS	33.59 ***	NS	NS	7.95 ***	NS
50 DAS	34.36 *	34.36 ***	45.83 **	NS	5.93 ***	NS

the lamp which affected the leaf chamber in spite of the fact that cool water was kept flowing below the lamp to dissipate its heat. Differences between the varieties were greater at 30 DAS than at 40 and 50 DAS.

Gas Exchange at the highest PPFD:

In this study, 100 mol m^{-3} NaCl salinity caused a decrease in Pn in both the varieties but the decrease was more in the salt-sensitive variety Punjab-85. This decrease was mainly due to a decrease in g_s, which was also decreased more in Punjab-85. The effects of salinity on Pn were greatest at 40 DAS when highest values were observed. At 40 DAS, salinity decreased Pn of LU26S by 14% and of Punjab-85 by 34% at the highest light intensity. Farquhar *et al.* (1989) and Iqbal (1992) reported a decrease in Pn and g_s when stress was experienced by the plant and decreases in Pn were reported to be due to decreases in g_s. Contrasting results were reported by Leidi *et al.* (1991b) who found that there were no effects of NaCl salinity up to 100 mol m^{-3} on the rate of Pn or E. They however reported a decrease in g_s with an increase in the levels of added NaCl in the growth medium. Kemal-ur-Rahim (1988) also reported that salinity had no effect on Pn at 120 mol m^{-3} NaCl. Another reason for lower Pn in Punjab-85 at 100 mol m^{-3} NaCl could be its higher Na^+ and Cl^- contents. Photosynthetic ability was inversely related to the concentration of either Na^+ or Cl^- in the leaves. Cl^- was reported to be more closely associated ($r^2 = 0.926$) with the inhibition of photosynthetic ability (Bethke and Drew, 1992). In this study also it was felt that the decrease in Pn due to NaCl stress was caused by osmotic effects on internal and mesophyll resistance (Kingsbury *et al.* 1984; Rawson, 1986) and also due to higher contents of Na^+ and Cl^- of the leaves especially in salt-sensitive variety Punjab-85.

Pn was higher at 40 DAS than at 30 or 50 DAS in both the varieties and at both the salinity levels and the lowest values were found at 50 DAS. This trend can not be explained however, simply on the basis of changes in g_s in LU26S because the pattern of decrease in Pn due to leaf age was different than that in g_s. At 30 DAS, g_s was higher than at 40 DAS. Marshall and Biscoe (1980b) also reported a decrease in Pn with the age of the leaves due to decrease in g_s. Decrease in g_s with an increase in leaf age was also noted at both the salinity levels and varieties. Changes in stomatal conductance have been mentioned as a reason for changes in Pn due to leaf age (Constable and Rawson, 1980). The reduction in Pn has also been associated with a decrease in g_s by Rawson and Woodward (1976).

Ci was not affected by salinity at any of the sampling dates but g_s was decreased. This indicates that the decrease in Pn due to salinity was also due to non-stomatal factors and that there was an adverse effect of 100 mol m^{-3} salinity on internal processes due to an increase in stomatal and mesophyll resistance (Kingsbury *et al.* 1984; Rawson, 1986). Excessive salts in the cytoplasm may also harm enzymes and organelles responsible for photosynthesis (Läuchli and Epstein, 1984) which may cause a decrease in Pn. Also at 40 and 50 DAS, Ci was higher in the salt-sensitive variety Punjab-85. Ci was generally higher at 50 than at 30 and 40 DAS in Punjab-85 possibly due to the decline in Pn associated with increased leaf age. In LU26S however, the effect of leaf age on Ci was not consistent. In contrast to the results noted in this study, Ci was reported to remain constant with leaf age by Davis and McCree (1978) suggesting that stomatal conductance was not affected by increasing CO_2 caused by a decrease in the internal conductance. A reduction in g_s is expected to cause a decrease in Pn by reducing the rate of CO_2 entry in the leaves and hence causing a decrease in Ci (Kemal-ur-Rahim, 1988).

There was a significant increase in Tl at 30 DAS due to 100 mol m^{-3} salinity in both the varieties and at 40 DAS in Punjab-85 only. The effect was more visible in the salt-sensitive variety Punjab-85. Presumably this is due to a lower cooling effect caused by lower g_s and E. The effect however was not consistent at 50 DAS. Iqbal (1992) reported an increase in Tl as a result of increasing time of exposure to NaCl salinity in the growth medium.

Gas Exchange Values calculated by Rectangular Hyperbola Model:

Net photosynthesis responds hyperbolically to PPFD as light becomes of decreasing importance as a limiting factor for photosynthesis. Individual leaves of many C_3 plants are unable to use additional light above 500-1000 μmol m^{-2} s^{-2} or roughly 25-50% of full sun light. The light saturated assimilation rate may be considered as a measure of the photosynthetic capacity of a leaf (Hall *et al.* 1993).

Pn_{max} values calculated by the rectangular hyperbola model were about 32 - 66% higher than the actual values of net photosynthesis (see Table - 5.4) but the trends followed were nearly the same. Kemal-ur-Rahim (1988) also reported a 57% over estimation of Pn_{max} by the rectangular hyperbola model in LU26S wheat variety at 120 mol m^{-3} NaCl stress. Pn_{max} was decreased by NaCl salinity especially at 40 DAS, in both varieties. In the salt-sensitive variety Punjab-85, I_c increased considerably at 30 and 40 DAS which was accompanied with a decrease in α. Although salt treated plants had a lower rate of respiration, they had higher light compensation point. In LU26S, α and I_c were comparatively unaffected which means that at low PPFD, salinity had a small effect and the effects of salinity were only apparent at high PPFD (see Fig 5.1). Decrease in Pn $_{max}$ by salinity in wheat has also been reported by different research workers (Rawson, 1986; Kemal-ur-Rahim, 1988; Iqbal, 1992). A decrease in Pn $_{max}$ with leaf age was also reported by Marshall and Biscoe (1980b). Iqbal (1992) reported a non-significant trend in α due to salinity but observed a decrease in α at the final measurement. In this study, the effect of 100 mol m^{-3} NaCl salinity on α was significant on the last sampling date only where it was about 24% higher in the leaves of the stressed plants than the non-stressed plants. However, Kemal-ur-Rahim (1988) reported that salinity had no affect on α in flag leaves nor on other leaves. Kemal-ur-Rahim (1988) reported an increase in I_c at 120 mol m^{-3} NaCl salinity in flag leaves as well as lower leaves in four wheat varieties. It is difficult to link changes in g_s with changes in R_d . Salinity consistently decreased g_s at 30, 40 and 50 DAS in both the varieties but R_d was decreased only at 30 and 40 DAS. An increase in R_d at 50 DAS could be due to high build up of ions (Na^+, K^+ and Cl^-) accompanied by senescence. The higher R_d in the salt-sensitive variety Punjab-85 seems to be partly due to lower g_s caused by high salinity stress and partly due to decrease in the internal conductance (Davis and McCree, 1978). However, increase in R_d due to salinity may not be explained simply on the basis of a decrease in g_s because then less O_2 diffuses in for respiration. Similar to the above findings, Rawson (1986) also reported a reduction in the younger leaves and an increase in the older leaves in R_d as a result of salinity stress in the leaves of barley.

Pn $_{max}$ values were very high as compared to the measured Pn values in spite of the fact that r^2 was very high. There could be two possible reasons for this discrepancy i.e.

1. Calculation of linear correlation does not take the intercept into account.
2. The assumption that Pn = Pg - R_d is erroneous at high PPFD values because photorespiration becomes an important component.

From the preceding discussion, it could be summed up that under salt stress, overall photosynthetic productivity was higher in LU26S than in Punjab-85 due to higher Pn, higher α, lower I_c and lower observed R_d, particularly at 40 and 50 DAS. It is also concluded that rectangular hyperbola model is not suitable for calculating Pn $_{max}$ and hence other Pn-I models like exponential model (Iqbal, 1992) may be used in future studies.

Effect of Salinity and Leaf Age on Ion Accumulation:

Na^+ contents of leaves in the two varieties did not differ significantly up to 40 DAS but at 50 DAS, the salt-sensitive variety Punjab-85 accumulated much higher amounts of Na^+ than the salt-tolerant variety LU26S . Schachtman and Munns (1992) and others (Salim, 1989, Salim, 1991; Sharma, 1991; Watanabe, 1992; Gorham *et al.* 1994; Khan, 1996) also reported that all the salt-tolerant accessions/cultivars in their experiments had lower rates of Na^+ accumulation. Comparatively lower contents of Na^+ at 30 and 40 DAS may be the result of higher rate of leaf growth (Schachtman and Munns, 1992). It has also been reported that there are at least two mechanisms that determine tolerance to NaCl i.e. low Na^+ uptake rates and the ability to tolerate high concentrations (Schachtman and Munns, 1992; Munns, 1993). Both of these mechanisms seem to play their role to impart better salt tolerance in LU26S.

Very high K^+ contents were noted in both the varieties but significantly higher amounts were accumulated in the salt-sensitive variety Punjab-85. It was found that at 100 mol m^{-3} NaCl salinity, K^+ contents increased over time in both the varieties. Although decreases in K^+ concentrations in the leaves in response to soil salinity in barley and also in wheat have been reported by many workers (Wyn Jones and Storey, 1978; Gorham *et al.* 1990; Iqbal, 1992; Khan, 1996); increases in salt affected plants of wheat have also been reported by a number of workers (Kemal-ur-Rahim, 1988; Iqbal, 1992; Gorham, 1994; Khan, 1996).

The mechanism of discrimination against Na^+ and for K^+ (Gorham, 1992, 1993, 1994) was noted in this study in both varieties. Gorham *et al.* (1990) reported that at low external salinities (< 100 mol m^{-3} NaCl), the enhanced K^+/Na^+ discrimination character results in low leaf Na^+ concentrations and maintenance of K^+ concentrations similar to those found in plants grown without stress. Munns (1993) and Munns *et al.* (1995) suggested that growth response to salinity occurs in two distinct phases which arise in sequence. During the first phase of osmotic effects, the growth reduction is similar but after many weeks there is a second phase when the salt-sensitive genotypes were reported to show greater reduction in growth due to salt specific effects. Higher K^+ contents in the leaf cell sap at higher salinity of 150 mol m^{-3} NaCl were also reported by Salam (1993) in some wheat cultivars.

It is possible that the optimum growing conditions in the growth room coupled with the loss of ion selectivity of the roots, as a result of increased Na^+/Ca^{2+} ratio (Greenway and Munns, 1980), resulted in high uptake K^+ and other ions. This might have increased the permeability of the root membranes to K^+ along with Na^+ and Cl^- which was responsible for increase of these ions in the cell sap. Higher uptake of K^+ at low external Na^+ concentration and lower uptake of K^+ at higher external Na^+ concentrations has also been reported in wheat (Khan, 1996).

K^+/Na^+ ratio was significantly lower at 100 mol m^{-3} NaCl in both the varieties than at 0 mol m^{-3} NaCl stress (Table - 5.7). The percent decreases at 30, 40 and 50 DAS were 47, 59 and 72 in salt-sensitive variety Punjab-85. In LU26S (salt-tolerant), the corresponding decreases were 44, 61 and 62%. There was lesser effect of age on the ratio up to 50 DAS in LU26S but at the same sampling date, a decrease of about 56% was noted in Punjab-85 than 40 DAS. Gorham (1994) also reported lower K^+/Na^+ ratios at 200 mol m^{-3} NaCl than at 50 mol m^{-3} NaCl in the growth medium. At 100 mol m^{-3} stress, the ratio was higher in the salt-sensitive variety Punjab-85 at 30 and 40 DAS, but at 50 DAS, K^+/Na^+ ratio in this variety was much lower than in LU26S which may be a reason for better salt-tolerance of the latter. The low K^+/Na^+ ratio in Punjab-85 at 50 DAS was mostly due to an increase in Na^+ contents and not due to a decrease in K^+ contents. This also indicates that mechanism of discrimination against Na^+ and for K^+ (Gorham, 1992, 1993, 1994) decreased with an increase in exposure of plants to salinity. A high K^+/Na^+ ratio in shoot has been also associated with better salt tolerance in wheat and tall wheat grass by Shannon (1978), Sharma (1991) and Qadar (1993).

Generally Ca^{2+} and Mg^{2+} contents were lower at 100 mol m^{-3} NaCl salinity than at 0 mol m^{-3} NaCl in both varieties while LU26S tended to maintain higher concentration of these ions. The trend for chloride was similar to the one noted for Na^+ but reverse of that noted in case of Mg^{2+}. Over all, high K^+, Na^+, Cl^- and low Ca^{2+} and Mg^{2+} contents were observed at 100 mol m^{-3} NaCl stress in both the varieties and the contents of toxic ions (Na^+ and Cl^-) were higher in Punjab-85 as compared to LU26S. Padole (1991) reported increased uptake of Na^+ and decreased uptake of K^+, Ca^{2+} and Mg^{2+} by salinity and/or sodicity of soil. LU26S had significantly higher Mg^{2+} at both the stress levels. Better capability to maintain higher amounts of Mg^{2+} in the cells has been associated with salt tolerance in wheat (Salama *et al.* 1994). In contrast to the results obtained in this study, Maas and Poss (1989) reported an increase in Ca^{2+} in plants grown in saline nutrient solution which may be due to an addition of extra $CaCl_2$ added to the nutrient solution.

Effect of Leaf Ion Contents on Photosynthesis:

With increase in salinity from 0 mol m^{-3} to 100 mol m^{-3} NaCl, Pn and g_s decreased at all the sampling dates while concentration of Na^+, Cl^- and K^+ increased (Table 5.8). Percentage increases in K^+ did not change much with leaf age and also were similar in both the varieties hence its role in changes of Pn is not clear (Table 5.9). Percentage increases in Na^+ and Cl^- contents due to NaCl stress on the other hand were very high and were still higher in the salt-sensitive variety Punjab-85. It seems as if accumulation of excessive amounts of Na^+ and Cl^- ions in the leaves were responsible for a decrease in g_s and then Pn. This interpretation however does not give a sufficient proof for the toxic effects of Na^+ and Cl^- ions on gas exchange because the percentage decreases in Pn were lesser than those in case of g_s and much smaller than the increase in Na^+ and Cl^- contents of the leaves. There was also, a slight effect of salinity on Ci (Table 5.2) which means that there were also increases in internal resistance at chloroplast level which were responsible for a decrease in Pn. A different trend was noted in Punjab-85 in the older leaves at 50 DAS where a considerable drop in Pn was noted even in the absence of NaCl stress which seemed to be due to more advanced senescence. It has been reported by different workers that rates of photosynthesis are usually lower in the plants grown in saline culture medium and it depends on the duration of exposure to NaCl (Walker *et al.* 1982; Yeo *et al.* 1985). As salt concentration in leaves increases with time of exposure, the reduction in Pn may be interpreted in terms of increasing salt toxicity (Yeo *et al.* 1985).

The above discussion indicates that in this study, the decrease in Pn was less due to reduced g_s and seemed to be non-stomatal in origin as has been reported by Bethke and Drew (1992). In the older leaves, the decrease in Pn especially in Punjab-85, seemed more due to senescence than NaCl stress alone. The reduction in Pn under salt stress is reported to be mostly due to an increase in stomatal and mesophyll resistance (Kingsbury *et al.* 1984; Rawson, 1986). Cl^- has also been reported to be closely associated ($r^2 = 0.926$) with the inhibition of photosynthetic ability (Bethke and Drew, 1992). Yeo *et al.* (1985) showed that Na^+ accumulation in the leaves of rice affected stomatal aperture and CO_2 fixation simultaneously. The reduced water potential generated by NaCl in the external medium can also affect stomata. Downton (1977) attributed decreases in Pn in the salt stressed grapevines to increased levels of Cl^- in the leaves which was responsible for increase in mesophyll resistance to CO_2 fixation.

Terry and Waldron (1984) reported that Pn was decreased by NaCl stress. Similar effect of NaCl stress have also been reported by Yeo *et al.* (1985), Rawson (1986), Yeo *et al.* (1991), Zerbi *et al.* (1991), Bethke and Drew (1992) and Iqbal (1992). Pn_{max} has also been reported to

Table - 5.8: Net photosynthesis (Pn) and g_s at the highest PPFD (μmol m^{-2} s^{-1}) of 2017±7.1 (30 DAS), 2015±11.3 (40 DAS), 2011±7.3 (50 DAS) and ion concentration in cell sap of 5th leaves in LU26S and Punjab-85

Leaf age	NaCl stress	LU26S					Punjab-85				
		Pn	g_s	Na^+	Cl^-	K^+	Pn	g_s	Na^+	Cl^-	K^+
30 DAS	0 mol m^{-3}	18.0	1.36	15.2	60.5	228	18.2	0.67	12.0	56.8	238
	100 mol m^{-3}	15.6	0.60	27.3	83.1	223	12.4	0.36	29.9	141.0	316
40 DAS	0 mol m^{-3}	19.7	0.60	11.5	54.7	285	19.4	0.79	11.2	55.6	296
	100 mol m^{-3}	16.9	0.42	35.1	166.7	369	12.8	0.30	35.7	228.8	410
50 DAS	0 mol m^{-3}	15.3	0.48	13.2	37.8	265	9.8	0.37	15.8	28.6	280
	100 mol m^{-3}	14.3	0.40	42.5	161.5	348	9.0	0.30	78.9	260.5	410

Table - 5.9: Percentage decreases (-) in net photosynthesis and g_s at the highest PPFD and increases (+) in ion concentration in cell sap of 5th. leaves in LU26S and Punjab-85 at 100 mol m^{-3} NaCl.

Leaf age	NaCl stress	LU26S					Punjab-85				
		Pn	g_s	Na^+	Cl^-	K^+	Pn	g_s	Na^+	Cl^-	K^+
30 DAS	100 mol m^{-3}	- 13	- 56	+ 80	+ 37	- 2	- 32	- 46	+ 149	+ 148	+ 33
40 DAS	100 mol m^{-3}	- 14	- 30	+ 205	+ 205	+ 29	- 34	- 62	+ 219	+ 312	+ 39
50 DAS	100 mol m^{-3}	- 7	- 2	+ 222	+ 327	+ 31	- 8	- 19	+ 399	+ 811	+ 46

decrease with an increase in Cl^- contents (Rawson, 1986). There are conflicting reports also which show that photosynthesis is not affected by salt concentrations up to 100 mol m^{-3} NaCl (Kemal-ur-Rahim, 1988; Leidi *et al.* 1991b).

Leidi *et al.* (1991b) reported a decrease in g_s with an increase in NaCl concentration in the growth medium. Decreases in net photosynthesis due to NaCl stress have also been reported in barley and wheat cultivars by Munns and Termaat (1986), Rawson (1986), Kalaji and Nalborczyk (1991), Zerbi *et al.* (1991) and Iqbal (1992).

Munns and Termaat (1986) argued that there is no evidence of a casual relationship between ion concentration and Pn; because when NaCl is removed from the growth medium, Pn recovers much more quickly than leaf salt concentration. They further argued that Pn may also be inhibited by reasons other than salt concentration in the leaves e.g. interaction of salts with ageing pattern of the leaves because NaCl hastens leaf senescence, the typical decline in Pn due to age and negative feedback on Pn by reduced sink activity. Nitrogen deficiency might occur in NaCl treated plants as Cl^- interferes with NO_3^- fluxes in roots causing a decreased NO_3^- concentration in leaves which might affect the Pn under salt stress.

5.5 CONCLUSIONS

The results obtained in this experiment confirmed the results of previous studies that NaCl salinity decreases the rate of net photosynthesis by affecting stomatal and non-stomatal factors. In the salt-sensitive variety, effect of leaf age was mainly due to non-stomatal factors which seem to be influenced by excessive concentrations of Na^+ and Cl^- in the leaves.

Fitting the rectangular hyperbola model for Pn/light response curves in wheat gave a good fit to the data (r^2 = 90 - 100%). It gave nearly a similar trend as found in case of Pn i.e. highest Pn was observed at 40 DAS, Pn decreased with salt stress and was greater in LU26S than Punjab-85 at 100 mol m^{-3} NaCl stress. However, it calculated 32-66% higher values for Pn_{max} as compared to actual observed values.

Photosynthetic efficiency (α) decreased with increase in leaf age while photon flux compensation point (I_c) increased with leaf age but the results were not conclusive. There was a decrease in the observed dark respiration (R_d) with increase in leaf age in the salt-tolerant variety LU26S. Ageing of the leaves had no effect on R_d in the salt-sensitive variety Punjab-85 in the absence of salt stress, while it increased with increase in leaf age at 100 mol m^{-3} NaCl.

Under salt stress, overall photosynthetic productivity was higher in the salt-tolerant variety LU26S than in the salt-sensitive variety Punjab-85 due to higher Pn, higher α, lower I_c and lower observed R_d , particularly in the older leaves.

K^+/Na^+ ratios in the salt-sensitive variety Punjab-85 were significantly higher than LU26S at 30 DAS but differences were non-significant at 40 and 50 DAS which indicates that K^+/Na^+ ratio may not be used as an indicator for salt tolerance in the younger plants especially under optimum growing conditions of the growth room or greenhouse. Increased uptake of Na^+, Cl^-, K^+ and decreased uptake of Ca^{2+} and Mg^{2+} was observed under salt stress.

CHAPTER 6

EFFECTS OF SALINITY AND pH OF THE CULTURE MEDIUM ON ION UPTAKE, GAS EXCHANGE AND GROWTH OF WHEAT UNDER HYDROPONIC CONDITIONS

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6.1 INTRODUCTION

The increasing demand for cereals and other food crops has necessitated the utilization of marginal lands with high salinity and having pH mostly in the alkaline range. In many instances, the demands to irrigate the increased cropped area has necessitated the use of brackish water with a high salt content and alkaline pH. Salt tolerance of wheat has been the focus of many workers for quite some time and has been studied quite extensively. Many scientists, however, have ignored the effect of high pH on crop growth in association with salt stress. In many arid regions of the world, including Pakistan, soils are mostly saline sodic and have a pH of 8.5 or more along with salt stress (Muhammad, 1993). These conditions cause nutrient imbalances in such soils, due to which the deleterious effects of salinity become more hazardous (Bajwa, 1993; Bandyopadhyay and Singh, 1993).

The effects of high salinity of the solution culture on different growth and gas exchange parameters have been described else where (see Chapter 1 and 2).

Alam (1981) studied the effects of different pH levels in solution culture ranging from 3.5 to 8.5 on rice growth and reported that growth was affected adversely at high pH and optimal dry matter accumulation was noted at pH levels between 5.5 and 6.5 . It was also reported that maximum reduction in growth occurred at both pH 3.5 and 8.5. Regarding internal nutrient balances, it was reported that Fe^{2+} concentration in the plants decreased with increasing solution pH while the concentration of other elements increased progressively.

Leidi *et al.* (1991a, b) studied the effect of high pH and salinity on wheat under NO_3^- and NH_4^+ nutrition. A decrease in wheat growth was reported with an increase in pH of the nutrient solution. Shoot dry weight declined with increasing NaCl concentration for nutrient solutions containing either form of nitrogen. Plant growth also decreased with an increase in pH, the effect being more pronounced in ammonium-fed plants. K^+ concentration in the shoots was reduced by increasing concentration of NaCl in the solution. A considerable decrease in K^+ was also noted at pH 9.0 and 100 mol m^{-3} NaCl salinity. High NaCl concentration and high pH in the nutrient solution resulted in an increase in Na^+ and Cl^- uptake. Findenegg *et al.* (1989) have reported an increase in free ammonium in sugar beet leaves at increased pH of the nutrient solution and suggested that ammonium accumulation could have been responsible for the growth depression obtained at high pH. The length of root hairs of wheat growing in Long Ashton nutrient solution was affected by pH and the concentration of Ca^{2+} . The length of root hair was decreased by high pH (>7.0) and by low Ca^{2+} concentration (Ewens and Leigh, 1985).

The majority of efficient nutrient solutions which are routinely used in solution culture studies, mostly have pH values between 5 and 6 and these limits are associated with healthy growth of many plants (Arnon and Hoagland, 1940), but do not represent the saline-sodic soil conditions (alkaline pH) encountered in the field. The pH limits at which injury occurs appears fairly well defined at somewhere about 3.0 - 3.5 for severe injury and 3.5 - 4.0 for marked depression in growth at the lower end of the scale, and at about 9.0 and 8.5 respectively at the upper end for wheat and barley in water culture (Hewitt, 1966). It was also reported that the effects of nitrates and ammonium nitrogen on pH changes of the nutrient solution are important for several reasons and depend on the percentages of ammonium and/or nitrate nitrogen in the nutrient solution. Minimum pH change in the nutrient solution occurred when the solution pH was at 6.0 which was attained when ammonium and nitrate nitrogen in the nutrient solution were supplied according to a ratio of 95:5 respectively. It has been documented that if all the nitrogen in the nutrient solution is in NO_3^- form there is a tendency of a rapid rise in solution pH as NO_3^- are absorbed (and other anions) at a fast rate accompanied by a similar absorption of H^+ ions or release of OH^- ions to maintain charge balances (Salisbury and Ross, 1991). In 24 hours, pH rose from 5.7 to 7.3 when all the nitrogen was supplied as NO_3^- to sunflower plants growing in nutrient culture. The pH problem can be minimized by supplying part of nitrogen as NH_4^+ salt because absorption of NH_4^+ and other cations occurs simultaneously with absorption of OH^- ions or transfer of H^+ from the root to the surrounding solution. A drop in pH from 5.5 to 4.5 was noted in 24 hours when nitrogen was supplied as a mixture of ¼ NO_3^- and ¾ NH_4^+ to the sunflower plants growing in solution culture (Salisbury and Ross, 1991).

At high pH values precipitation of iron compounds is likely and availability of calcium, phosphorus and in some cases manganese may also decrease (Guest and Chapman, 1944; Salisbury and Ross, 1991).

The purpose of this preliminary experiment was to study the effects of salinity at high (alkaline) and low (acidic) pH on wheat, to find out if the pH of the hydroponic culture medium influences responses to salt stress.

6.2 MATERIALS AND METHODS

6.2.1 Experimental Material

Plastic pots of 10 litre capacity with expanded polystyrene tops, were used for growing the plants. The pots as well as the lids were painted black to discourage any fungal growth. Twelve holes were bored in the polystyrene lids to hold the seedlings. The variety SARC-1 was chosen as its performance under salt stress was comparatively superior to other tested varieties in a previous experiment conducted in a glasshouse (see sections 2.3.3, 2.3.7 and 2.3.8).

6.2.2 Glass house Conditions

This experiment was conducted in a glasshouse at University College of North Wales, College Farm, Aber, Gwynedd, UK from March 27, 1995 to May 11, 1995. The average maximum and minimum daily temperatures in the glasshouse during the course of this study were 30.1±1.1 and 8.1±0.5°C respectively. During the same period, average sunshine hours at the farm were 6.4±0.6 hours.

6.2.3 Sowing of the Seeds

Seeds of SARC-1 variety of wheat were germinated on capillary matting placed over a plastic pot which was filled to the top with tap water according to the procedures described in Chapter 5. The seeds were placed for germination in a walk-in growth room on March 27, 1995. After germination, 12 healthy seedlings were transplanted into each polystyrene lid and held in place with pieces of foam.

6.2.4 Nutrient Solution

Nutrient solution was introduced 3 days after transplanting. The nutrient solution contained 5.0 g of Phostrogen per 10 litre water to which trace elements were added according to modified Long Ashton formula (Hewitt, 1966). Fe was added as Fe-EDDHA from a stock solution (instead of Fe-EDTA) @ 4.0 mg l^{-1} to the nutrient solution in the pots to improve the iron availability to the plants under alkaline pH conditions (Leidi *et al.* 1991a). Iron is more easily available to plants from Fe-EDDHA than other Fe-chelates (Nabhan *et al.* 1977; Chaney, 1988). In this experiment, pH level of the fresh culture solution in the pots was close to 5.8 and it dropped to about 5.0 in seven days at which time the solutions were changed.

6.2.5 Salt and pH stress

Two salt stress levels i.e. 0 mol m^{-3} NaCl (control) and 100 mol m^{-3} NaCl were tested. At each stress level, two pH levels i.e. pH 5.8 (pH of freshly prepared nutrient solution) and 8.5 were imposed. Salt stress levels were produced by adding calculated amounts of commercial NaCl to the nutrient solution. pH levels were adjusted to 8.5 by adding 1.0 M KOH. Salt was added starting 7 days after transplanting at the rate of 25 mol m^{-3} NaCl per day and was raised up to 100 mol m^{-3}. The two pH levels were imposed at the time when the salt stressed plants were at 100 mol m^{-3} NaCl. The treatments thus produced were as follows.

1. 0 mol m^{-3} NaCl at pH 5.8 (control)
2. 0 mol m^{-3} NaCl at pH 8.5
3. 100 mol m^{-3} NaCl stress at pH 5.8
4. 100 mol m^{-3} NaCl stress at pH 8.5

To raise the solution pH, KOH was used instead of NaOH to avoid excessive build up of Na^+ in the solution keeping in mind its toxicity (Richards, 1969).

For bringing the pH to 8.5, about 19 to 20 ml. of 1.0 M KOH had to be added to each pot on the first day after changing the solutions. The KOH was added in 5 ml. portions and when it was close to 8.5, in 1 ml. portions in each pot and pH was noted with a portable pH metre each time. The exact amount of KOH to be added was slightly different for each pot due to slightly different rates of aeration and different mass of roots in different pots. Once the pH was adjusted to 8.5, it dropped considerably to around 7.0 within 24 hours. This was thought to be due to continuous aeration of the nutrient solution and root activity. On the subsequent days, lesser amount of KOH was needed to raise the pH to 8.5 which ranged from 3 to 4 ml. daily. Slight precipitation was noted in the nutrient solution even in pots at low pH but it was quite high in pots kept at pH 8.5 and 100 mol m^{-3} NaCl salinity due to higher concentration of salts and high pH.

To avoid excessive build up in K^+ in the pots at high pH and for proper nutrient balance in the growth medium, nutrient solutions were changed after every week. Leidi *et al.* (1991a) also changed nutrients solutions after every week while Alam (1981) changed the solutions after every three days.

To study the effect of aeration and root growth on change of pH of solution culture, a small scale study was conducted which showed that there was no pH change in the nutrient solutions in the absence of aeration and living plant roots. The pH decreased from 5.8 to 5.3 in a seven day period in the pots kept under continuous aeration without any growing plants. Maximum drop in solution pH from 5.8 to 5.0 during the same period was noted in the pots containing growing plants and kept under continuous aeration. The greater reduction in pH in the pots containing the living plants might be due to the root exudates (H^+) released in the solution by the plant roots as they took up cations from the culture solution.

6.2.6 Maintenance of the Experiment

Nutrient solutions were kept under constant aeration and were changed after every week as described under Chapter 5. pH 8.5 was maintained daily with 1.0 M KOH while the lower pH level was left undisturbed. The pots were topped daily with tap water to make up the loss due to evapotranspiration.

6.2.7 Visual Observations

Crop growth appeared normal in all the treatments during the first 3 - 4 weeks. Visual observations showed that crop growth (height of plants, biomass and tillering) were greatest at pH 8.5 in the absence of NaCl stress as compared to other treatments. After that symptoms of iron deficiency (pale green colour and interveinal chlorosis) were observed in the plants growing at pH 8.5. These symptoms were quite severe at pH 8.5 in association with 100 mol m^{-3} NaCl stress and at the time of harvest, senescence was much advanced in this treatment as compared to other treatments. Root growth was affected adversely at pH 8.5 both at 0 mol m^{-3} and 100 mol m^{-3} NaCl stress. The roots were short, discoloured and had fewer root hairs at high pH.

6.2.8 Infra Red Gas Analyser (IRGA)

Gas exchange measurements were made using a portable Infra-red gas analyser (IRGA-Model LCA-2), on the sixth, fully expanded leaf on the main stem, 45 days after sowing. The IRGA was set up according to the procedures described in Chapter 5, and the same leaf chamber was used for these measurements. Gas exchange measurements were made at a PPFD of 1000 ± 30 μmol m^{-2} s^{-1} by shifting the plants to a growth room. The pots were allowed to equilibrate under artificial light for about half an hour before recording the readings. These measurements were made on four plants in each treatment from each replication according to the procedures described in Chapter 5.

After measuring gas exchange, the remaining plants were harvested to record agronomic data i.e. number of tillers, leaf area, shoot dry weight and root dry weight. The samples of shoot and root were dried in an oven at 80°C for 72 hours and dry weights were then recorded.

6.2.9 Ion Analysis

Sap was extracted for ion analysis from the same leaves on which gas exchange measurements were made. After recording the gas exchange measurements, these leaves were washed in distilled water, blotted to remove the excess water and then placed in polypropylene microcentrifuge tubes and stored in a freezer at -10 °C for ion analysis.

The procedures followed for cell sap extraction and the determination of Na^+, K^+, Ca^{2+}, Mg^{2+} and Cl^- are described in Chapter 5.

6.2.10 Statistical Analysis

The experiment was laid out in a completely randomised design with five replications. All the data were analysed by analysis of variance, and means and standard errors of means (SE) were calculated by Minitab statistical programme (version 10.2). An example of the anova table is presented in Appendix 6.1. LSD values were calculated according to the formula given in Chapter 5. LSD values for Na^+ and K^+/Na^+ ratios were calculated according to Chapter 3 (see section 3.2.5).

6.3 RESULTS

6.3.1 Gas Exchange Parameters

Both salinity and high pH resulted in significant decreases in Pn and g_s. The salinity x pH interaction was not significant. For both Pn and g_s the effects of salinity were greater than the effects of high pH.

At 0 mol m^{-3} NaCl Pn decreased by 26% as a result of increase in pH from 5.8 to 8.5 (Table 6.1). At 100 mol m^{-3} stress, the decrease in Pn was 42%. The lowest rate of net photosynthesis was observed at 100 mol m^{-3} NaCl in association with pH 8.5.

Stomatal conductance (g_s), was affected in a similar way. Compared to the control g_s was decreased by 26%, 53% and 70% at pH 8.5, 100 mol m^{-3} NaCl stress and 100 mol m^{-3} stress + pH 8.5 respectively (Table 6.1).

Data regarding transpiration (E) are presented in Table - 6.2. The decreases in E were smaller than the decreases in Pn and g_s but again the effects of salinity were greater than the effects of high pH. Compared to the control, E was decreased by 14%, 28% and 48% at pH 8.5, 100 mol m^{-3} NaCl stress and 100 mol m^{-3} stress + pH 8.5 respectively. The effects of salinity and pH were highly significant but their interaction was non-significant.

The recorded sub-stomatal CO_2 (Ci) is presented in Table 6.2. Ci was significantly higher at pH 8.5 than at pH 5.8. The effect of salinity and salinity x pH interaction were non-significant. Salinity resulted in a slight but significant increase in leaf temperature (Table 6.2). The effects of pH and salinity x pH interaction were non-significant.

6.3.2 Agronomic Data

The effects of salt stress and pH on the number of tillers per plant at 45 DAS, are presented in Table - 6.3. At pH 8.5, there was a 22% increase in the number of tillers per plant compared to the control. At 100 mol m^{-3} NaCl, there was a 49% decrease in the number of tillers, while at 100 mol m^{-3} NaCl + pH 8.5 the effect was most severe and the decrease was 56% compared to the control. The effects of salinity, pH and the salinity x pH interaction were significant.

Leaf area per plant (Table 6.3) showed a similar trend. An increase of 22% was noted at pH 8.5, compared to a decrease of 62% at 100 mol m^{-3} NaCl. At 100 mol m^{-3} stress + pH 8.5, the leaf area was affected more adversely and a decrease of 74% was noted in this case. The effects of salinity and salinity x pH were highly significant but the effects of pH were non-significant.

Table - 6.1: Effect of salinity and pH on net photosynthesis (Pn; μmol CO_2 m^{-2} s^{-1}) and stomatal conductance (g_s; mol m^{-2} s^{-1}) in SARC-1 wheat at 45 DAS.

Treatments		Pn		g_s	
NaCl stress	pH	Means	± SE	Means	± SE
0 mol m^{-3}	5.8	15.5	0.26	0.48	0.04
0 mol m^{-3}	8.5	11.4	0.39	0.36	0.02
100 mol m^{-3}	5.8	9.0	0.29	0.23	0.01
100 mol m^{-3}	8.5	5.8	0.24	0.15	0.01
Salinity means					
0 mol m^{-3}		13.5	0.41	0.42	0.02
100 mol m^{-3}		7.4	0.32	0.19	0.01
pH Means					
pH 5.8		12.2	0.56	0.36	0.03
pH 8.5		8.6	0.50	0.25	0.02

LSD values at $p = 0.05$

Parameters	NaCl salinity	pH	salinity x pH
Pn	0.61 ***	0.61 ***	NS
g_s	0.04 ***	0.04 ***	NS

- The salinity x pH values are means of twenty observations.
- The salinity and pH values are means of forty observations.

*** = significant at $p<0.001$

Table - 6.2: Effect of salinity and pH on transpiration (E; mmol m^{-2} s^{-1}), sub-stomatal carbon dioxide (Ci; $\mu l\ l^{-1}$) and leaf temperature (°C) in SARC-1 wheat.

Treatments		E		Ci		Leaf temperature	
NaCl stress	pH	Means	± SE	Means	± SE	Means	± SE
0 mol m^{-3}	5.8	7.49	0.24	231	3.8	24.3	0.25
0 mol m^{-3}	8.5	6.47	0.19	241	2.5	24.6	0.23
100 mol m^{-3}	5.8	5.42	0.21	232	3.5	25.3	0.27
100 mol m^{-3}	8.5	3.86	0.15	241	2.8	25.4	0.26
Salinity means							
0 mol m^{-3}		6.98	0.17	236	2.38	24.5	0.17
100 mol m^{-3}		4.64	0.18	236	2.30	25.4	0.18
pH means							
pH 5.8		6.45	0.23	231	2.54	24.8	0.19
pH 8.5		5.16	0.24	241	1.87	25.0	0.18

LSD values at p = 0.05

Parameters	NaCl salinity	pH	salinity x pH
E	0.40 ***	0.40 ***	NS
Ci	6.45 NS	6.45 **	NS
Leaf temperature	0.50 **	NS	NS

- The salinity x pH values are means of twenty observations.
- The salinity and pH values are means of forty observations.

*** = significant at p<0.001

** = significant at p<0.01

Table - 6.3: Effect of salinity and pH on the number of tillers and leaf area (cm^2) per plant in SARC-1 wheat at 45 DAS.

Treatments		Number of tillers		Leaf area	
NaCl stress	pH	Means	± SE	Means	± SE
0 mol m^{-3}	5.8	6.4	0.28	379	21.9
0 mol m^{-3}	8.5	7.8	0.25	460	27.7
100 mol m^{-3}	5.8	3.3	0.14	143	15.0
100 mol m^{-3}	8.5	2.8	0.15	98	10.8
Salinity means					
0 mol m^{-3}		7.1	0.20	419	18.8
100 mol m^{-3}		3.1	0.10	121	9.9
pH means					
pH 5.8		4.8	0.22	261	24.8
pH 8.5		5.3	0.29	279	35.7

LSD values at p = 0.05

Parameters	NaCl salinity	pH	salinity x pH
Number of tillers	0.42 ***	0.42 *	0.59 ***
Leaf area	40.61 ***	NS	56.3 **

- The salinity x pH values are means of fifty observations for number of tillers and sixteen observations for leaf area.
- The salinity and pH values are means of 100 observations for number of tillers and 32 observations for leaf area.

*** = significant at $p<0.001$
** = significant at $p<0.01$
* = significant at $p<0.05$

Dry weight of shoots per plant at 45 DAS is presented in Table - 6.4. Dry weight of shoots was decreased by 6% due to an increase of pH alone but by 55% due to 100 mol m^{-3} NaCl. The decrease was highest (77%) at pH 8.5+100 mol m^{-3} NaCl stress. The effects of salinity and pH were highly significant while those of salinity x pH were non-significant.

In the case of dry weight of roots per plant the effects of pH were small compared to the effects of salinity (Table - 6.4). Averaged over the two pH levels, salinity decreased root dry weight by 56%. The lowest dry weight of roots was noted at 100 mol m^{-3} NaCl + pH 8.5 and in this case the decrease in dry weight was 63% as compared to control. The effects of salinity were highly significant while those of pH and salinity x pH interaction were non-significant.

Effect of salinity and pH on shoot:root ratio is presented in Table 6.5. Increased salinity and pH of the solution culture caused significant decreases in shoot:root ratio of 20% and 17% respectively. The effect of salinity x pH was however, found to be non-significant.

Specific leaf area (Table - 6.5) was significantly decreased by NaCl salinity and significantly increased at high pH but the effects of salinity x pH were not significant. There was an increase in specific leaf area at high pH at both the salinity levels. The increase noted at high pH at both the salinity levels was about 16% as compared to low pH.

6.3.3 Ions in Leaf Sap

Sodium content was markedly greater at 100 mol m^{-3} NaCl than at 0 mol m^{-3} NaCl (Table - 6.6). At both the pH levels, Na^+ content was the same in the absence of salt stress while at 100 mol m^{-3} salt stress, it was 12% higher at pH 8.5 than at pH 5.8. However, these differences were non-significant.

Salinity resulted in a significant decrease in K^+ content at both pH levels (Table - 6.6). Increased pH also resulted in a significant decrease in the K^+ contents. The decrease at increased salinity level (100 mol m^{-3} NaCl) was 38% as compared to 0 mol m^{-3} NaCl. The decrease in K^+ content due to higher pH level was 14%. The salinity x pH interaction was non-significant which shows that effect of salinity was similar at both the pH levels.

Table - 6.4: Effect of salinity and pH on the dry weight (g) of shoots and roots per plant in SARC-1 wheat at 45 DAS.

Treatments		Dry weight shoots		Dry weight roots	
NaCl stress	pH	Means	± SE	Means	± SE
0 mol m^{-3}	5.8	2.49	0.20	0.65	0.08
0 mol m^{-3}	8.5	2.34	0.16	0.67	0.06
100 mol m^{-3}	5.8	1.11	0.13	0.35	0.08
100 mol m^{-3}	8.5	0.58	0.05	0.24	0.04
Salinity means					
0 mol m^{-3}		2.42	0.13	0.66	0.05
100 mol m^{-3}		0.85	0.08	0.29	0.04
pH means					
pH 5.8		1.80	0.17	0.50	0.08
pH 8.5		1.46	0.18	0.46	0.09

LSD values at p = 0.05

Parameters	NaCl salinity	pH	salinity x pH
Dry weight shoots	0.30 ***	0.30 *	NS
Dry weight roots	0.06 ***	NS	NS

- The salinity x pH values are means of 16 observations for dry weight shoots and four observations for dry weight roots.
- The salinity and pH values are means 32 observations for dry weight shoots and 8 observations for dry weight roots.

*** = significant at $p<0.001$

* = significant at $p<0.05$

Table - 6.5: Effect of salinity and pH stress on shoot:root and specific leaf area ($cm^2\ g^{-1}$) in SARC-1 wheat at 45 DAS.

Treatments		Shoot:root		Specific leaf area	
NaCl stress	pH	Means	± SE	Means	± SE
0 mol m^{-3}	5.8	3.81	0.25	271	5.11
0 mol m^{-3}	8.5	3.49	0.21	316	7.13
100 mol m^{-3}	5.8	3.37	0.26	207	13.12
100 mol m^{-3}	8.5	2.44	0.17	240	8.13
Salinity means					
0 mol m^{-3}		3.65	0.16	293	6.33
100 mol m^{-3}		2.91	0.17	223	8.14
pH means					
pH 5.8		3.59	0.18	239	7.32
pH 8.5		2.97	0.16	278	9.18

LSD values at p = 0.05

Parameters	NaCl salinity	pH	salinity x pH
Shoot:root	0.45 **	0.45 **	NS
Specific leaf area	17.74 ***	17.74 ***	NS

- The salinity x pH values are means of twenty observations for shoot:root ratio and 16 values for specific leaf area.
- The salinity and pH values are means of forty observations for shoot:root ratio and 32 values for specific leaf area..

*** = significant at $p<0.001$
** = significant at $p<0.01$

Table - 6.6: Effect of salinity and pH on Na^+, K^+ (mol m^{-3})and K^+/Na^+ ratios in cell sap at 45 DAS in SARC-1 wheat at 45 DAS.

Treatments		Na^+		K^+		K^+/Na^+ ratio	
NaCl stress	pH	Means	± SE	Means	± SE	Means	± SE
0 mol m^{-3}	5.8	4	0.1	291	5.4	67.7	1.5
0 mol m^{-3}	8.5	4	0.2	251	5.9	60.7	4.7
100 mol m^{-3}	5.8	213	12.5	211	18.6	1.1	0.1
100 mol m^{-3}	8.5	238	13.2	131	7.7	0.6	0.1
Salinity means							
0 mol m^{-3}		4	0.1	271	5.1	64	2.5
100 mol m^{-3}		225	9.2	171	11.8	1	0.1
pH means							
pH 5.8		109	17.8	251	11.5	34	5.4
pH 8.5		121	19.8	191	10.7	31	5.3

LSD values at $p = 0.05$

Parameters	LSD
Na^+ (0 mol m^{-3} NaCl)	NS
Na^+ (100 mol m^{-3} NaCl)	NS
K^+/Na^+(0 mol m^{-3} NaCl)	NS
K^+/Na^+(100 mol m^{-3} NaCl)	0.26 *

Parameters	NaCl salinity	pH	Salinity x pH
K^+	21.8 ***	21.8 ***	NS

- The salinity x pH values for K^+ are means of twenty observations.
- The salinity and pH values are means of forty observations.

*** = significant at $p<0.001$

Increased pH caused a considerable decrease in K^+/Na^+ (Table 6.6). The ratio was significantly higher (45%) at pH 5.8 than pH 8.5, at 100 mol m^{-3} NaCl salinity. At 0 mol m^{-3} NaCl, there was a decrease of about 10% at pH 8.5 as compared to pH 5.8, but the differences were found to be non-significant.

Ca^{2+} content was decreased significantly at 100 mol m^{-3} NaCl (Table 6.7) but the effects of pH and salinity x pH interaction were found to be non-significant.

Mg^{2+} content was decreased significantly by salinity and significantly increased at high pH level (Table 6.7).

Cl^- content was significantly increased by both salinity and high pH level (Table 6.7). The increase due to salinity was very high (about five times of control i.e. 0 mol m^{-3} NaCl salinity + pH 5.8) while the increase in Cl^- content due to higher pH alone was comparatively low. The increase in Cl^- contents caused by high pH in the absence of salinity was 35% while this increase was 13% in the presence of 100 mol m^{-3} NaCl salinity.

6.4 DISCUSSION

Wheat and barley are reported to suffer a reduction in growth at pH 8.5 and 9.0 respectively (Hewitt, 1966). In spite of the fact that Fe-EDDHA was used as source for Fe^{2+} which has a better availability under alkaline conditions (Nabhan *et al.* 1977; Chaney, 1988), the plants kept at pH 8.5 showed some chlorosis. This paleness and slight chlorosis of leaves could be due to a decrease in chlorophyll concentration in the leaves of wheat with increase in pH of the culture medium as reported by Leidi *et al.* (1991a). Pale colour of the leaves could also be due to disturbance in nitrogen nutrition at high pH (Leidi *et al.* 1991b). Ratio of ammonical and nitrate nitrogen in Phostrogen which was used for nutrient supply, is 80:20 which is near to the recommended ratio of 95:5 (Hewitt, 1966).

Many factors influence photosynthesis in the plants i.e. H_2O, CO_2, light, nutrients and temperature, as well as plant age and genotype (Salisbury and Ross, 1991). In this study, different NaCl concentrations and pH of the nutrient solutions affected various gas exchange parameters, agronomic characters and ion contents of the cell sap to variable degrees and these are discussed in the following paragraphs.

Table - 6.7: Effect of salinity and pH on Ca^{2+}, Mg^{2+} and Cl^- (mol m^{-3}) in cell sap at 45 DAS in SARC-1 wheat.

Treatments		Ca^{2+}		Mg^{2+}		Cl^-	
NaCl stress	pH	Means	± SE	Means	± SE	Means	± SE
0 mol m^{-3}	5.8	4.9	0.2	16.5	1.0	24.3	1.5
0 mol m^{-3}	8.5	4.8	0.3	26.4	1.0	32.9	1.9
100 mol m^{-3}	5.8	1.6	0.1	7.8	0.5	108.9	6.9
100 mol m^{-3}	8.5	1.8	0.1	12.8	1.1	123.3	5.6
Salinity means							
0 mol m^{-3}		4.8	0.2	21.5	1.0	28.6	1.4
100 mol m^{-3}		1.7	0.1	10.3	0.7	116.1	4.5
pH Means							
pH 5.8		NS		12.2	0.9	66.6	7.6
pH 8.5		NS		19.6	1.3	78.1	7.8

LSD values at p = 0.05

Parameters	NaCl salinity	pH	salinity x pH
Ca^{2+}	0.39 ***	NS	NS
Mg^{2+}	1.73 ***	1.73 ***	2.41 **
Cl^-	9.31 ***	9.31 *	NS

- The salinity x pH values are means of twenty observations.
- The salinity and pH values are means of forty observations.

*** = significant at $p<0.001$
** = significant at $p<0.01$
* = significant at $p<0.05$

Gas Exchange Parameters:

At 100 mol m^{-3} NaCl salinity, a significant reduction in Pn was observed which was accompanied by a parallel decrease in g_s and E. Salinity increased the Tl but Ci stayed unaffected. A decrease in g_s with no changes in Ci indicated that decreases in Pn were mostly due to an increase in stomatal and mesophyll resistance (Kingsbury *et al.* 1984; Rawson, 1986). Reduced transpiration due to impaired g_s at 100 mol m^{-3} NaCl may be responsible for elevation of leaf temperature (Terry and Waldron, 1984). High pH of the nutrient solution also caused a decrease in Pn, g_s and E while Tl remained unaffected. High pH was responsible for a significant increase in Ci which may be due to inhibition in CO_2 fixation at chloroplast level (Läuchli and Epstein, 1984). The decreases in these parameters caused by salinity were greater than those caused by high pH. The effects of salinity were greater at high pH than at low pH and caused greater decreases in Pn, g_s and E although the salinity x pH interaction was non-significant. In contrast to this, Leidi *et al.* (1991b) found that in NH_4^+ fed plants, E decreased at high NaCl concentration and increased with an increase in pH of the nutrient solution. On the other hand, g_s was decreased with increasing levels of NaCl concentration and this decrease was further enhanced at high pH. In this experiment, there was no effect of NaCl salinity on the Ci while a significant increase was caused by high pH. This indicates that high pH may be responsible for slowing down the photosynthetic process which caused an increase in Ci. The inhibition in Pn seemed to be due to the presence of some internal resistance (Bethke and Drew, 1992), in the plants grown at high NaCl concentration and high pH. Similar decrease in g_s due to NaCl stress was reported by Leidi *et al.* (1991b) which was further decreased by high pH.

Leidi *et al.* (1991b) reported a decrease in chlorophyll concentration in the leaves of wheat with increase in pH of the culture medium containing NaCl. Decrease in chlorophyll contents of the leaves (Salama *et al.* 1994) might have been responsible for a decrease in Pn at high pH in this study. Khan (1996) reported non-significant decreases in Pn at high ESP of the soil which was reported to have a pH greater than 8.5 (Richards, 1969).

Agronomic Parameters:

Salinity generally reduces growth of crop plants through its effect on the shoot and root growth, decrease in leaf area, number and length of tillers and dry matter accumulation (Munns and Termaat, 1986; Salim, 1989; Läuchli and Epstein, 1990; Shalhevet *et al.* 1995). Soil pH has been reported to be an important factor influencing the growth of most field crops and pastures (Christenson *et al.* 1971). The effect of soil pH is associated with changes in the solubility and availability of plant nutrients.

At pH 5.8, salinity decreased number of tillers and leaf area by 48% and 62% respectively compared to control (S_0 $pH_{5.8}$). However at pH 8.5, the corresponding decreases were 64% and 79%. Hence the effects of salinity on these parameters were considerably greater at high pH than at low pH, and also substantially greater on leaf area than on the number of tillers. It is clear from this, that decrease in total leaf area per plant was due to a decrease in the number of tillers as well as a decrease in the area of individual leaves. Number of tillers and leaf area per plant increased at pH 8.5 in the absence of NaCl stress. This might be due to higher K^+ level in this treatment and comparatively better nutrition because KOH solution was added to raise the pH of the nutrient solution. However, this is unlikely as K^+ in leaf sap was lower at pH 8.5 than at pH 5.8. In contrast to the above, Leidi *et al.* (1991a) did not observe this trend in their experiment on wheat. Salinity is responsible for reduction in leaf growth which mainly occurs at low salinities and in this way it affects yield adversely (Wyn Jones and Gorham, 1989; Iqbal, 1992). The effects of salinity are mediated largely by changes in the plant's water status particularly that of the leaf. An increase in root zone salinity would aggravate this effect by lowering the overall water status of the plants. It has also been reported that water deficit in the expanding tissues of barley as a result of salinity stress was responsible for decreased plant growth (Delane *et al.* 1982; Munns *et al.* 1982).

With increase in age and build up of the salt concentration other symptoms of salt injury may appear. The specific effects of salinity on leaf and other growth parameters under saline conditions could be due to excessive transport of Na^+ and Cl^- and decreased uptake of K^+, Ca^{2+}, Mg^{2+}, NO_3^- or SO_4^{2-} ions (Termaat and Munns, 1986). The adverse effects of salinity may be further aggravated at high pH of the growth medium (Srivastava, 1988; Leidi *et al.* 1991a). A growth inhibition was observed by Findenegg *et al.* (1989) in sugar beet both at high pH and at increased Cl^- concentration.

Percent decreases in shoot weight and root weight due to salinity were greater at high pH than at low pH. Dry weight of shoots decreased by salinity by about 55% at pH 5.8 and about 75% at pH 8.5. Dry weight of roots was also affected considerably by salinity and the decreases were about 46% at low pH and 64% at high pH. Here also, the effect of salinity were greater at high pH than at low pH. The effects of salinity and high pH were greater on shoots than on roots.

The effect of pH on dry weight of roots however was non-significant. The combined effects of salinity and high pH were greater than salinity alone on both of these parameters.

The effect of the treatments on shoot:root ratio was similar to that noted in case of dry weight of shoots. The decrease in shoot:root ratio suggests that the effects of salinity and high pH were greater on shoots than on roots. Leidi *et al.* (1991a) reported that ratio of shoot to root dry weight of wheat was not affected up to 100 mol m^{-3} NaCl salinity. Tang and Robson (1993) reported a reduction in the growth of roots and shoots in *Lupinus* species with increasing pH of hydroponic culture medium above 6.0, which resulted in decreased uptake of Fe^{2+} and phosphorus. A substantial decrease in growth of rice tops and roots at pH 8.5 was also reported by Alam (1981). Devitt *et al.* (1984) also reported a decrease in wheat root weight in response to an increase in osmotic potential of the nutrient solution.

Specific leaf area was decreased by 100 mol m^{-3} NaCl salinity. There was a non-significant increase at higher pH at 0 mol m^{-3} and 100 mol m^{-3} NaCl which shows that leaves were comparatively thinner at high pH.

Ion Concentrations in Cell Sap:

Salt tolerance in crops such as wheat and barley is generally determined by their capabilities to exclude Na^+ and Cl^- from their shoots and their ability to maintain high shoot K^+ concentrations. This indicates the presence and operation of certain mechanisms in the plants which affect the transport processes which discriminate against Na^+ and favour the uptake of K^+ (Gorham, 1994). An increase in the uptake of Cl^- at high pH level of the nutrient solution was reported by Findenegg *et al.* (1989) in sugar beet. Wheat cultivars resistant to salinity and/or sodicity of soil were reported to maintain a lower concentration of Na^+ and higher concentration of K^+ and K^+/Na^+ ratio than the sensitive cultivars (Sharma, 1991). Uptake of N, P, K^+, Ca^{2+}, Mg^{2+}, Zn^{2+}, Mn^{2+}, Cu^{2+} and Fe^{2+} were reduced by salinity and/or sodicity in wheat (Padole, 1991). Srivastava and Srivastava (1993) conducted a pot study and found that as soil pH increased from 7.2 to 10.3 levels of water soluble and exchangeable Fe^{2+} decreased while levels of iron oxides increased.

In this study, Na^+ and Cl^- concentrations in the leaves were significantly increased at 100 mol m^{-3} NaCl salinity. Na^+ content was not affected at high pH in the absence of NaCl salinity. However, at 100 mol m^{-3} NaCl salinity, pH 8.5 caused about 12% increase in Na^+ contents. High pH also resulted in enhanced uptake of Cl^- at both the salinity levels. However in both cases, salinity x pH interaction was non-significant. The increase in the Na^+/Ca^{2+} ratio in the solution by added NaCl may have resulted in increased permeability of the root membranes to Na^+ and Cl^- due to a loss in root selectivity (Greenway and Munns, 1980). Increase in Na^+ content in the leaf sap with high NaCl concentration of the growth medium has been reported by many workers (Gorham *et al.* 1986; Munns and Termaat, 1986; Sharma, 1989; Azmi and Alam, 1990; Padole, 1991; Salim, 1991; Iqbal, 1992; Watanabe *et al.* 1992; Schachtman and Munns, 1992; Akhtar *et al.* 1994). Leidi *et al.* (1991a) reported an increase in Na^+ and Cl^- contents at high NaCl concentration and high pH of the nutrient solution. In an experiment conducted in pots by Sharma (1991) to compare Kharchia-65 (resistant) and HD 4502 (sensitive) wheat varieties at different ESP levels, it was found that plant Na^+ concentration was greater in the sensitive than in the tolerant variety. At pH 9.4 and 9.6, Na^+ concentration in the leaves of salt-sensitive HD4502 was >2% while in Kharchia-65 (resistant), all leaves had <2% Na^+. Yasin (1991) reported an increase in leaf Na^+ and a decrease in K^+ contents with increasing Na^+ and ESP of the soil in PAK-81 and Rawal-87 wheat varieties.

K^+ concentration of the leaves was reduced by high salinity as well as high pH. {At pH 5.8, salinity caused a 27% decrease in K^+ while corresponding decrease at high pH was 48%. This shows that the combined effect of high salinity and high pH caused a major decrease in K^+ contents of the leaves. Reduced K^+ uptake has been often reported in wheat plants growing in solution culture containing NaCl (Munns and Termaat, 1986; Iqbal, 1992; Watanabe *et al.* 1992; Gorham, 1994). Similar results of high NaCl concentration and high pH on K^+ uptake were also reported by Leidi *et al.* (1991a) in wheat and Alam (1981) in rice. The effect of high pH in decreasing K^+ concentration is surprising in this study, as pH of the nutrient solution was raised by adding KOH.

K^+/Na^+ ratio was drastically decreased by 100 mol m^{-3} NaCl salinity. A slight decrease was also caused by high pH at 0 mol m^{-3} NaCl (about 10%) and at 100 mol m^{-3} NaCl (about 45%) i.e. percent decrease in K^+/Na^+ ratio was quite high due to combined effect of high pH and NaCl salinity. Khan (1996) observed similar decrease in K^+/Na^+ in the leaf cell sap of wheat genotypes grown in culture medium containing NaCl.

Ca^{2+} and Mg^{2+} of the cell sap was decreased by NaCl salinity. There was no effect of high pH on Ca^{2+} contents while Mg^{2+} contents were increased significantly by high pH at both the salinity levels. Na^+ is known to displace Ca^{2+} at root membranes (Cramer *et al.* 1985) which might be a cause for decreased Ca^{2+} in the leaf cell sap of the NaCl treated plants. Results in this study for Ca^{2+} uptake are in contrast to those of Leidi *et al.* (1991a) who reported that concentration of Ca^{2+} in the shoots of wheat decreased with increasing pH of the growth medium containing nitrate as a source of nitrogen. An increase in Ca^{2+} and Mg^{2+} uptake with increasing pH in tops and roots of rice plants has also been reported by Alam (1981). Sufficient membrane damage may occur in roots at high pH to allow the loss of previously absorbed nutrients by the plants (Alam, 1981). Kirkby and Mengel (1967) also found that changes in pH of the nutrient medium and the type of nitrogen supplied affected the ion uptake of plants.

6.5 CONCLUSIONS

The data obtained in this study provide some (but inconclusive) evidence that the effects of salinity on Pn, growth and uptake of toxic ions are greater at high pH than at low pH. Percentage decreases in root and shoot weight, leaf area due to salinity were greater at high pH than at low pH. Increases in concentrations of toxic ions were also greater at high pH than at low pH. A salt-tolerant variety SARC-1 was used in this experiment. The following experiment reported in Chapter - 7, is a repeat of this experiment using both salt-sensitive and salt-tolerant wheat varieties. pH 8.5 in combination with 100 mol m^{-3} NaCl proved very harmful for the plants in this experiment. Hence in the following experiment, pH 8.0 was used to enable the crop to grow up to maturity.

CHAPTER 7

EFFECTS OF SALINITY AND pH OF THE CULTURE MEDIUM ON GROWTH, GAS EXCHANGE AND ION UPTAKE IN TWO WHEAT VARIETIES HAVING CONTRASTING CHARACTER OF SALT TOLERANCE IN SOLUTION CULTURE

CHAPTER 7

EFFECTS OF SALINITY AND pH OF THE CULTURE MEDIUM ON GROWTH, GAS EXCHANGE AND ION UPTAKE IN TWO WHEAT VARIETIES HAVING CONTRASTING CHARACTER OF SALT-TOLERANCE IN SOLUTION CULTURE

7.1 INTRODUCTION

The preliminary experiment reported in Chapter 6 was conducted to study the effect of salinity at high and low pH of the nutrient solution and to identify the problems encountered when growing plants at high pH in the culture medium. The results of that experiment provided some evidence that the adverse effects of salinity were greater at high pH than at low pH.

During the course of that study it was observed that at pH 8.5 in the presence of 100 mol m^{-3} NaCl stress, there was some precipitation in the nutrient solution compared to other treatments. Symptoms of nutrient deficiency (pale colour and chlorosis of leaves and in some younger leaves interveinal chlorosis was also observed), possibly due to deficiency of iron, manganese or zinc were also evident in this treatment towards the later stages of the experiment.

Hence in this experiment, it was planned to use pH 8.0 instead of 8.5 . It was aimed to study the effect of these treatments on gas exchange parameters, ion uptake and agronomic parameters including grain yield on the two wheat varieties having contrasting characteristics of salt tolerance i.e. LU26S (salt tolerant) and Punjab-85 (salt sensitive) and were used in earlier experiments reported in this thesis. Measurements were made for uptake of toxic ions (Na^+ and Cl^-) and K^+, Ca^{2+}, Mg^{2+} , Zn^{2+} , Fe^{2+} and Mn^{2+} to evaluate the effects of salinity and high pH on these parameters.

7.2 MATERIALS AND METHODS

7.2.1 Growth Conditions

The experiment was conducted in a glasshouse at University College of North Wales, College Farm, Aber, Gwynedd, UK from June 12, 1995 to September 1, 1995. Ten litre plastic pots were used in this experiment. Pots were painted black to discourage algal growth. Lids of these pots were made of expanded polystyrene. In each lid, 16 holes were bored with the help of hot cork borer. The lids were then also painted black. Capillary matting was pasted on the lower surface of the polystyrene tops using Copydex glue. These lids were used for planting the seeds. The temperature in the glasshouse during the study period ranged from a minimum of 9.0 °C to a maximum of 46.0 °C. Average maximum and minimum temperatures during the course of this study were 35.8 °C and 14.2 °C respectively. Sunshine hours recorded at the farm observatory during the course of this study ranged from 0.0 hours per day to 16.0 hours per day with an average value of 7.6 hours per day.

7.2.2 Experimental Material and Sowing

Two wheat varieties having contrasting tolerance to salinity i.e. LU26S (salt tolerant) and Punjab-85 (salt sensitive) were selected for this study (see Chapter 5).

The seeds were soaked for 24 hours in water in a flask starting on June 12, 1995 and were kept under constant aeration during this period. Next day i.e. June 13, 1995 the imbibed seeds were sown in the holes of the polystyrene lids. The holes were filled with vermiculite up to about 0.5 cm depth. The seeds were then placed in the hole over it and were covered to the top with vermiculite. This method of sowing was used to avoid transplanting shock to the seedlings. Pots were then filled with tap water up to top to keep the seeds and vermiculite moist. The tops were covered with paper to avoid excessive evaporation due to high temperature to facilitate germination. The treatments were replicated five times. Two replications were used for gas exchange measurements and growth analysis while the remaining three replications were grown up to maturity. Final harvesting was completed on September 1, 1995.

7.2.3 Salt and pH stress

Two stress levels i.e. 0 mol m^{-3} NaCl (control) and 100 mol m^{-3} NaCl were tested as was done in the previous experiment (Chapter 6). The two pH levels tested were pH 6.0 and 8.0. The amount of 1.0 M KOH needed to raise the pH of the nutrient solution to 8.0 was about 17.0 -18.0 ml. on the first day and 3-5 ml. daily on the subsequent days. Other procedures were the same as described in Chapter 6. The following treatments were thus produced.

Treatments

	Varieties	NaCl stress	pH	
1.	LU26S	0 mol m^{-3}	6.0	($S_0pH_{6.0}$) ... (control for LU26S)
2.	LU26S	0 mol m^{-3}	8.0	($S_0pH_{8.0}$)

3.	LU26S	100 mol m^{-3}	6.0	($S_{100}pH_{6.0}$)
4.	LU26S	100 mol m^{-3}	8.0	($S_{100}pH_{8.0}$)
5.	Punjab-85	0 mol m^{-3}	6.0	($S_0pH_{6.0}$) ... (control for Punjab-85)
6.	Punjab-85	0 mol m^{-3}	8.0	($S_0pH_{8.0}$)
7.	Punjab-85	100 mol m^{-3}	6.0	($S_{100}pH_{6.0}$)
8.	Punjab-85	100 mol m^{-3}	8.0	($S_{100}pH_{8.0}$)

7.2.4 Nutrient Solution

Nutrition solution was prepared and used as in Chapter 6. Nutrient solutions in all the respective pots were raised to pH 8.0 with the help of 1 M KOH. pH was monitored daily with a portable pH metre and adjusted using KOH. The pH of the treatments at pH 6.0 was not maintained and it decreased slightly during the 7 days before the next change of solutions. Nutrient solutions were changed after every 7 days.

7.2.5 Maintenance of the experiment

Growth of LU26S was faster than that of Punjab-85 initially and due to its luxuriant growth, this variety suffered an early attack of mildew and aphids. This attack was mild on Punjab-85 initially but later on it was also affected by mildew and aphids. These problems were controlled by use of appropriate agrochemicals applied at the recommended rates.

7.2.6 Visual Observations

Very good plants were obtained under the new method of planting and the plants escaped the transplantation shock also, which was noted in the previous experiments. The treatments at high pH without salinity had more tillers and the main shoots were longer than the controls ($S_0pH_{6.0}$) and NaCl-stressed treatments. However, the plants were less green than control plants ($S_0pH_{6.0}$) in both varieties. The treatments having 100 mol m^{-3} NaCl along with pH 8.0 ($S_{100}pH_{8.0}$) were affected the most and the growth was also very stunted. Chlorosis developed at high pH but the symptoms developed later as compared to the experiment described in Chapter 6. At 60 DAS, senescence was much more advanced in the $S_{100}pH_{6.0}$ and $S_{100}pH_{8.0}$ and more so in Punjab-85. The root development was affected adversely at high pH and 100 mol m^{-3} NaCl stress. Root growth was affected at pH 8.0 both at 0 mol m^{-3} and 100 mol m^{-3} NaCl stress. The roots were short, discoloured and had fewer root hairs at high pH while at pH 6.0, the roots appeared healthy. In both the varieties growth was best in $S_0pH_{6.0}$ and worst at $S_{100}pH_{8.0}$.

7.2.7 Gas Exchange Measurements

Gas exchange data were recorded at 37 DAS on fully expanded 6th leaves using plants from two replicates. Six plants were used from each pot (12 plants from each treatment) for this purpose. Measurements were taken according to the procedures described under Chapter 6. PPFD for recording these data were 1080 ± 25 μmol m^{-2} s^{-1}. After completing the gas exchange measurements, 6th leaves were removed from the plants, washed in distilled water, blotted dry to remove excess water and were then placed in polypropylene microcentrifuge tubes and stored in a freezer at -10 °C for extraction of sap and ion measurements. The same plants (excluding roots) were harvested, washed in distilled water, blotted to remove excess water, placed in paper bags, then dried in an air oven and dry weights recorded as described under Chapter 6. These samples were later on used for ion analysis on dry weight basis.

7.2.8 Growth Analysis

From the same replicates where gas exchange data was recorded , another six plants were harvested at 38 DAS from each pot (12 plants from each treatment) for recording growth analysis data i.e. number of tillers per plant, leaf area, fresh and dry weight per plant, dry weight of roots and specific leaf area.

Leaf laminae were detached from the main stem, weighed, and leaf area was measured by automatic leaf area meter (Model AAM7, Hayashi Denkoh Co. Ltd., Tokyo, Japan). After measuring leaf area, the leaves were placed inside labelled paper bags and placed in an oven along with the stems at 80°C for 72 hours and dry weights were then recorded.

Qualitative green leaf area was assessed at 60 DAS, two weeks before the final harvest, to estimate the effect of treatments on this important parameter. Grading was done according to the percentage of total green leaf area in the plants and green flag leaf area in the plants in all the three replications using four plants from each pot as given below.

Grade 1	0 - 20% green leaf area
Grade 2	21 - 40% green leaf area
Grade 3	41 - 60% green leaf area

Grade 4 61 - 80% green leaf area

Grade 5 81 -100% green leaf area

These grades were also statistically analysed along with the other data.

7.2.9 Sampling of the Leaves and Sap Extraction For Ion Analysis

The 6th leaves sampled from plants after gas exchange measurements (see section 7.2.6) were used for sap extraction according to the procedures described in Chapter 6.

7.2.10 Ion Analysis from Cell Sap

Na^+, K^+, Ca^{2+}, Mg^{2+} and Cl^- in extracted leaf sap were determined according to the procedures described in Chapter 6 (Section 6.2.9).

7.2.11 Ion Analysis From Dried Plant Material

Preparation of Samples:

The dried plants (see section 7.2.7) were ground in a mill and 0.5 g samples of the ground plant material were weighed into crucibles and ashed in a furnace at 400 °C for four hours.

Acid Digestion of Samples:

After cooling of the furnace the crucibles were taken out of the furnace and were placed in a desiccator. The ash was dissolved in 10 ml. (2 x 5 ml. portions) of 4 M HNO_3 and transferred in a 20 ml. volumetric flask. Crucibles were then washed twice with distilled water and the washings transferred to the volumetric flask and the volume made up. After making the appropriate dilutions Na^+, K^+, Ca^{2+}, Mg^{2+} and Cl^-were determined according to the procedures described in Chapter 6 (Section 6.2.9). The trace elements Fe^{2+}, Zn^{2+} and Mn^{2+} were determined by atomic absorption spectrophotometer at 249, 213.9 and 279 nm wave length respectively using Pye Unicam SP9 model of atomic absorption spectrophotometer.

7.2.12 Yield and Yield Components

Three replicates were allowed to mature. Eighteen plants were harvested from each treatment (six plants from each pot) by cutting at the base of the plants (excluding roots). Data regarding number of tillers per plant, number of ears per plant, length of main shoots from base of stem to tip of ears, weight of plants, fertile and sterile spikelets per plant, number and weight of grains per plant and 100 grain weight were recorded.

7.2.13 Statistical analysis

The experiment was laid out in a completely randomised design with five replications. All the data were analyzed by analysis of variance, and means and standard errors of means (SE) were calculated by Minitab statistical programme (version 10.2). Examples of the anova tables are presented in Appendix 7.1 - 7.3. LSD values were calculated according to the formula given in Chapter 5 except Na^+ and K^+/Na^+. LSD values for Na^+ and K^+/Na^+ ratios were calculated according to the procedure described in Chapter 3 (section 3.2.5).

7.3 RESULTS

The analysis of variance showed that generally the effects of 100 mol m^{-3} NaCl salinity were significant for the majority of the parameters. Significant differences were found in both the varieties in case of Pn, ion contents and qualitative green leaf area at 60 DAS. The effect of pH was found significant only for Ci, Na^+, K^+, Cl^-, root dry weight, shoot:root ratio, qualitative green leaf area, Na^+, K^+, Ca^{2+}, Zn^{2+} and Mn^{2+} in the dried plant material. Interactions between the factors were mostly non-significant except variety x salinity interactions which were significant for some ions and agronomic parameters. The salinity x pH interaction was rarely significant indicating that the effects of salinity were the same at high and low pH. The variety x salinity x pH interaction was also rarely significant, indicating that the effects of salinity and pH were generally the same on both the salt-sensitive and salt-tolerant variety.

7.3.1 Gas Exchange Parameters

Pn and g_s :

Data for Pn and g_s is presented in Table 7.1. LU26S had a significantly higher rate of photosynthesis than Punjab-85. Salinity decreased Pn significantly ($p<0.001$), while there was no significant effect of high pH on Pn. The lowest rate of net photosynthesis was observed at 100 mol m^{-3} NaCl in association with pH 8.0 ($S_{100}pH_{8.0}$) in LU26S and at 100 mol m^{-3} NaCl ($S_{100}pH_{6.0}$) in Punjab-85 variety. All the interactions between different factors were non-significant. g_s was not affected by any factor and the effects of variety, stress, pH and all the interactions were found to be non-significant.

Table - 7.1: Effect of salinity and pH of the culture solution on net photosynthesis (Pn; μmol CO_2 m^{-2} s^{-1}) and stomatal conductance (g_s; mol m^{-2} s^{-1}) in LU26S and Punjab-85 wheat varieties at 37 DAS.

		Pn				g_s			
Treatments		LU26S		Punjab-85		LU26S		Punjab-85	
NaCl stress	pH	Means	± SE	Means	± SE	Means	± SE	Means	± SE
0 mol m^{-3}	6.0	15.8	0.76	14.7	0.91	0.52	0.04	0.48	0.05
0 mol m^{-3}	8.0	15.0	1.06	13.4	0.90	0.54	0.05	0.42	0.04
100 mol m^{-3}	6.0	12.1	0.82	9.4	0.65	0.36	0.04	0.37	0.06
100 mol m^{-3}	8.0	11.4	1.17	10.8	0.66	0.52	0.04	0.43	0.06

Variety means									
LU26S		13.6	0.54						
Punjab-85		12.1	0.49						

NaCl means									
0 mol m^{-3}		14.7	0.46						
100 mol m^{-3}		10.9	0.44						

LSD values at $p = 0.05$

Parameters	V	S	pH	V*S	V*pH	S*pH	V*S*pH
Pn	1.25 *	1.25 ***	NS	NS	NS	NS	NS
g_s	NS	NS	NS	NS	NS	NS	NS

- All values (V*S*pH) are means of twelve observations.
- All values for variety, NaCl stress and pH means are averages of 48 observations.

*** = significant at $p<0.001$

* = significant at $p<0.05$

Rate of transpiration (E) and sub-stomatal CO_2 (Ci) :

Data regarding the effects of salinity, pH and varieties on the rate of transpiration and sub-stomatal CO_2 is presented in Table 7.2. Rate of transpiration was similar in both the varieties and at both the levels of salinity and pH. All the interactions were also non-significant except salinity x pH which was significant at $p<0.05$. This showed that higher pH had non-significant effect at S_0 but increased E significantly at S_{100}. This trend was visible in both the varieties.

High salinity and high pH significantly increased Ci (concentration of sub-stomatal CO_2). There was however no effect on varietal means. All the interactions were non-significant except variety x pH. This showed that Ci was similar in Punjab-85 in $S_0pH_{6.0}$ and $S_0pH_{8.0}$ treatments and was high at $S_{100}pH_{6.0}$ and $S_{100}pH_{8.0.}$ In LU26S, Ci was significantly similar in $S_0pH_{6.0}$, $S_0pH_{8.0}$ and $S_{100}pH_{6.0}$ but was significantly higher in $S_{100}pH_{8.0}$ than the other treatments.

Leaf temperature (Tl):

The effects of variety, salinity, pH on Tl, and all the interactions except variety x pH were found to be non-significant (Table 7.3). Significant interaction of variety x pH showed that varieties responded differently to the levels of pH. In LU26S, Tl was significantly lower at $S_0pH_{8.0}$ but there was a significant increase in the salt sensitive variety Punjab-85. Effects of higher pH at S_{100} were however, non-significant in both the varieties.

7.3.2 Growth Analysis at 38 DAS

Number of tillers and leaf area :

The data presented in Table 7.4 highlight the effect of salinity and pH on number of tillers and leaf area per plant. Variety Punjab-85 had significantly higher number of tillers than LU26S while 100 mol m^{-3} NaCl salinity significantly decreased number of tillers per plant. Although the effect of pH level was non-significant, the effects of variety x salinity and variety x pH were found to be significant while other interactions were non-significant. The number of tillers in LU26S were not significantly decreased by salinity but in Punjab-85, a significant decrease was noted where number of tillers decreased by about 48% at 100 mol m^{-3} NaCl salinity. A different and opposite effect was noted in case of variety x pH interaction, where number of tillers decreased at higher pH level (non-significant effect) in LU26S but there was a significant increase (16%) in the salt-sensitive variety Punjab-85.

Table - 7.2: Effect of salinity and pH of the culture solution on transpiration (E; mmol $m^{-2} s^{-1}$) and sub-stomatal CO_2 (Ci; $\mu l\ l^{-1}$) in LU26S and Punjab-85 wheat varieties at 37 DAS.

		E				Ci			
Treatments		LU26S		Punjab-85		LU26S		Punjab-85	
NaCl stress	pH	Means	± SE	Means	± SE	Means	± SE	Means	± SE
0 mol m^{-3}	6.0	8.96	0.35	8.89	0.47	222	3.94	228	3.35
0 mol m^{-3}	8.0	8.22	0.51	8.55	0.38	229	5.16	226	4.20
100 mol m^{-3}	6.0	7.12	0.40	8.12	0.87	226	3.80	240	7.87
100 mol m^{-3}	8.0	8.49	0.27	9.00	0.76	250	6.07	245	5.06

NaCl means									
0 mol m^{-3}						226			
100 mol m^{-3}						240			

pH means									
pH 6.0						229			
pH 8.0						238			

S x pH means		pH 6	pH 8						
0 mol m^{-3}		8.9	8.4						
100 mol m^{-3}		7.6	8.8						

V x pH means						pH 6	pH 8		
LU26S						225	228		
Punjab-85						233	247		

LSD values at p = 0.05

Parameters	V	S	pH	V*S	V*pH	S*pH	V*S*pH
E	NS	NS	NS	NS	NS	1.11 *	NS
Ci	NS	7.28 ***	7.28 *	NS	10.55 *	NS	NS

- All values (V*S*pH) are means of twelve observations.
- All values for variety, NaCl stress and pH means are averages of 48 observations.

*** = significant at p<0.001

* = significant at p<0.05

Table - 7.3: Effect of salinity and pH of the culture solution on leaf temperature (Tl; °C) in LU26S and Punjab-85 wheat varieties at 37 DAS.

		Leaf temperature (Tl)			
Treatments		LU26S		Punjab-85	
NaCl stress	pH	Means	± SE	Means	± SE
0 mol m^{-3}	6.0	27.8	0.33	26.9	0.35
0 mol m^{-3}	8.0	26.2	0.30	27.9	0.53
100 mol m^{-3}	6.0	27.1	0.50	27.2	0.32
100 mol m^{-3}	8.0	26.5	0.33	27.1	0.37
V x pH		pH 6	pH 8		
LU26S		27.5	26.3		
Punjab-85		27.1	27.5		

LSD values at p = 0.05

Parameters	V	S	pH	V*S	V*pH	S*pH	V*S*pH
Tl	NS	NS	NS	NS	0.80 **	NS	NS

- All values (V*S*pH) are means of twelve observations.
- All values for variety, NaCl stress and pH means are averages of 48 observations.

** = significant at $p<0.01$

Table - 7.4: Effect of salinity and pH of the culture solution on number of tillers and leaf area (cm^2) per plant in LU26S and Punjab-85 wheat varieties at 38 DAS.

Treatments		Number of tillers				Leaf area			
		LU26S		Punjab-85		LU26S		Punjab-85	
NaCl stress	pH	Means	± SE	Means	± SE	Means	± SE	Means	± SE
0 mol m^{-3}	6.0	4.6	0.40	7.3	0.62	334	15.0	374	27.6
0 mol m^{-3}	8.0	4.2	0.24	8.8	0.49	327	20.2	384	32.4
100 mol m^{-3}	6.0	3.7	0.22	4.3	0.38	155	10.1	116	9.0
100 mol m^{-3}	8.0	3.6	0.19	4.7	0.28	153	7.9	124	6.8
Variety means									
LU26S		4.0							
Punjab-85		6.3							
NaCl means									
0 mol m^{-3}		6.2				355			
100 mol m^{-3}		4.1				137			
V x S		0 mol m^{-3} NaCl		100 mol m^{-3} NaCl		0 mol m^{-3} NaCl		100 mol m^{-3} NaCl	
LU26S		4.4		3.6		330		154	
Punjab-85		8.1		4.5		379		120	
V x pH		pH 6		pH 8					
LU26S		4.1		3.9					
Punjab-85		5.8		6.7					

LSD values at p = 0.05

Parameters	V	S	pH	V*S	V*pH	S*pH	V*S*pH
Tillers	0.54 ***	0.54 ***	NS	0.78 ***	0.78 *	NS	NS
Leaf area	NS	26.3 ***	NS	38.1 **	NS	NS	NS

- All values (V*S*pH) are means of twelve observations.
- All values for variety, NaCl stress and pH means are averages of 48 observations.

*** = significant at $p<0.001$

** = significant at $p<0.01$

* = significant at $p<0.05$

Leaf area was significantly decreased by 100 mol m^{-3} NaCl while the effect of variety and pH was non-significant. Variety x salinity interaction was also significant in leaf area while all the other interactions were non-significant. This showed that leaf area was significantly higher in the salt-sensitive variety Punjab-85 than LU26S at low salinity (0 mol m^{-3} NaCl) but was higher in the salt-tolerant variety LU26S at 100 mol m^{-3} NaCl salinity.

For both leaf area and tiller number averaged over the two pH levels, the percentage decreases at high salinity were greater in Punjab-85 (69% and 44% respectively) than in LU26S (54% and 17% respectively).

Fresh weight and dry weight per plant :

Both fresh weight and dry weight per plant were decreased significantly ($p<0.001$) at 100 mol m^{-3} NaCl salinity (Table 7.5). Effects of variety and pH were non-significant in both of these parameters but variety x salinity interaction was significant for fresh weight as well as dry weight per plant. All the other interactions were non-significant. Averaged over the two pH levels, percentage decreases in fresh weight and dry weight, caused by 100 mol m^{-3} NaCl salinity were greater in Punjab-85 (69% and 58% respectively) than in LU26S (53% and 41% respectively). Differences between varieties were non-significant at 0 mol m^{-3} salinity but were significant at 100 mol m^{-3} NaCl salinity.

Dry weight of roots per plant :

Dry weight of roots per plant (Table 7.6) was decreased significantly as a result of higher level of NaCl salinity and pH. Dry weight of roots was also significantly higher in the salt-tolerant variety LU26S than the salt-sensitive variety Punjab-85. Effects of variety x salinity and salinity x pH were highly significant ($p<0.001$) while other interactions were non-significant. Differences between varieties were not significant at 0 mol m^{-3} salinity but were significant at 100 mol m^{-3} NaCl salinity and decreases were greater in Punjab-85 than LU26S. Similarly, there was a significant decrease in root dry weight at 0 mol m^{-3} salinity at higher pH but at 100 mol m^{-3} salinity, there was a non-significant increase at pH 8.0.

Table - 7.5: Effect of salinity and pH of the culture solution on fresh weight and dry weight per plant (g) in LU26S and Punjab-85 wheat varieties at 38 DAS.

		Fresh weight				Dry weight			
Treatments		LU26S		Punjab-85		LU26S		Punjab-85	
NaCl stress	pH	Means	± SE	Means	± SE	Means	± SE	Means	± SE
0 mol m^{-3}	6.0	13.95	0.83	13.83	1.27	1.93	0.12	1.98	0.21
0 mol m^{-3}	8.0	13.29	0.90	15.06	1.10	1.83	0.16	2.18	0.14
100 mol m^{-3}	6.0	6.30	0.46	4.42	0.40	1.07	0.09	0.84	0.09
100 mol m^{-3}	8.0	6.47	0.45	4.61	0.30	1.14	0.09	0.90	0.06
NaCl means									
0 mol m^{-3}		14.03				1.98			
100 mol m^{-3}		5.45				0.99			
V x S means		0 mol m^{-3} NaCl		100 mol m^{-3} NaCl		0 mol m^{-3} NaCl		100 mol m^{-3} NaCl	
LU26S		13.62		6.39		1.88		1.11	
Punjab-85		14.45		4.51		2.08		0.87	

LSD values at $p = 0.05$

Parameters	V	S	pH	V*S	V*pH	S*pH	V*S*pH
F. weight	NS	1.12 ***	NS	1.63 *	NS	NS	NS
Dry weight	NS	0.18 ***	NS	0.27 *	NS	NS	NS

- All values (V*S*pH) are means of twelve observations.
- All values for variety, NaCl stress and pH means are averages of 48 observations.

*** = significant at $p<0.001$

* = significant at $p<0.05$

Table - 7.6: Effect of salinity and pH of the culture solution on dry weight root per plant (g) and specific leaf area (cm^2/g dry weight) in LU26S and Punjab-85 wheat varieties at 38 DAS.

		Dry weight root				Specific leaf area			
Treatments		LU26S		Punjab-85		LU26S		Punjab-85	
NaCl stress	pH	Means	± SE	Means	± SE	Means	± SE	Means	± SE
0 mol m^{-3}	6.0	0.42	0.01	0.43	0.00	291	7.5	329	4.9
0 mol m^{-3}	8.0	0.34	0.00	0.35	0.00	312	9.0	331	21.2
100 mol m^{-3}	6.0	0.32	0.01	0.27	0.01	312	5.8	294	7.0
100 mol m^{-3}	8.0	0.33	0.01	0.30	0.00	290	7.7	294	6.4
Variety means									
LU26S		0.36							
Punjab-85		0.34							
NaCl means									
0 mol m^{-3}		0.39				316			
100 mol m^{-3}		0.31				298			
pH means									
pH 6.0		0.36							
pH 8.0		0.33							
V x S means		0 mol m^{-3} NaCl		100 mol m^{-3} NaCl		0 mol m^{-3} NaCl		100 mol m^{-3} NaCl	
LU26S		0.38		0.32		330		154	
Punjab-85		0.39		0.28		379		120	
S x pH means		pH 6.0		pH 8.0					
0 mol m^{-3} NaCl		0.43		0.35					
100 mol m^{-3} NaCl		0.30		0.32					

LSD values at $p = 0.05$

Parameters	V	S	pH	V*S	V*pH	S*pH	V*S*pH
D.wt. root	0.01 **	0.01 ***	0.01 ***	0.02 ***	NS	0.02 ***	NS
S. L. area	NS	14.16 *	NS	20.53 *	NS	NS	NS

- All values (V*S*pH) are means of twelve observations.
- All values for variety, NaCl stress and pH means are averages of 48 observations.

*** = significant at $p<0.001$, ** = significant at $p<0.01$

* = significant at $p<0.05$

Specific leaf area :

Specific leaf area was decreased significantly ($p<0.001$) by 100 mol m^{-3} NaCl salinity while the effects of variety and pH were non-significant (Table 7.6). Variety x salinity interaction was significant i.e. the varieties responded differently to salinity levels. Specific leaf area was significantly greater in Punjab-85 than in LU26S at 0 mol m^{-3} NaCl salinity but was similar at 100 mol m^{-3} salinity. At 100 mol m^{-3} NaCl salinity the decrease in specific leaf area in the salt-tolerant variety LU26S was non-significant while a significant decrease was noted in the salt-sensitive variety Punjab-85. All the other interactions were found to be non-significant.

Fresh weight : dry weight ratio :

Fresh weight : dry weight ratio (Table 7.7) was significantly decreased by 100 mol m^{-3} NaCl salinity but the effect of pH was non-significant. This ratio was significantly higher in LU26S than Punjab-85. This shows that LU26S was able to maintain significantly higher succulence at both the salinity levels. All the interactions were non-significant.

Shoot : root ratio :

Shoot : root ratio significantly decreased at 100 mol m^{-3} NaCl salinity but increased at pH 8.0 (Table 7.7) but the varietal differences were non-significant. Salinity x pH interaction was also significant at $p<0.05$. This shows that response to changes in pH was different at different salinity levels. Shoot : root ratio was significantly higher in $S_0pH_{8.0}$ than $S_0pH_{6.0}$ but was similar in $S_{100}pH_{6.0}$ and $S_{100}pH_{8.0}$. The ratio was also significantly lower in $S_{100}pH_{6.0}$ and $S_{100}pH_{8.0}$ as compared to the non-stressed treatments ($S_0pH_{6.0}$ and $S_0pH_{8.0}$). All the other interactions were non-significant.

Qualitative grading of green leaf area at 60 DAS :

Towards the maturity of the crop, it was noted that senescence was much more advanced in Punjab-85 than in LU26S especially at elevated NaCl salinity both at low and high pH level. Hence qualitative grading for green leaf area was made for all the leaves and flag leaves of the plants and the results are presented in Table 7.8. Total green leaf area and green flag leaf area was significantly decreased as a result of 100 mol m^{-3} salinity and increased at higher pH. At 60 DAS, salt-tolerant variety LU26S had significantly higher total green leaf area as well as green flag leaf

Table - 7.7: Effect of salinity and pH of the culture solution on ratios of fresh weight:dry weight and shoot:root in LU26S and Punjab-85 wheat varieties at 38 DAS.

		Fresh weight:dry weight				Shoot:root			
Treatments		LU26S		Punjab-85		LU26S		Punjab-85	
NaCl stress	pH	Means	± SE	Means	± SE	Means	± SE	Means	± SE
0 mol m^{-3}	6.0	7.26	0.15	7.08	0.17	4.63	0.37	4.62	0.50
0 mol m^{-3}	8.0	7.40	0.22	7.03	0.58	5.28	0.42	6.24	0.40
100 mol m^{-3}	6.0	5.92	0.09	5.33	0.11	3.42	0.34	3.10	0.27
100 mol m^{-3}	8.0	5.72	0.08	5.10	0.04	3.42	0.23	3.01	0.17
Variety means									
LU26S		6.58							
Punjab-85		6.13							
NaCl means									
0 mol m^{-3}		7.19				5.20			
100 mol m^{-3}		5.52				3.24			
pH means									
pH 6.0						3.94			
pH 8.0						4.49			
S x pH means						pH 6		pH 8	
0 mol m^{-3} NaCl						4.63		5.76	
100 mol m^{-3} NaCl						3.26		3.21	

LSD values at p = 0.05

Parameters	V	S	pH	V*S	V*pH	S*pH	V*S*pH
F.wt:D.wt.	0.34 *	0.34 ***	NS	NS	NS	NS	NS
Shoot:root	NS	0.50 ***	0.50 *	NS	NS	0.72 *	NS

- All values (V*S*pH) are means of twelve observations.
- All values for variety, NaCl stress and pH means are averages of 48 observations.

*** = significant at $p<0.001$

* = significant at $p<0.05$

Table - 7.8: Effect of salinity and pH of the culture solution on estimated proportions of green leaf area and green flag leaf area (qualitative grading) in LU26S and Punjab-85 wheat varieties at 60 DAS.

		Green leaf area				Green flag leaf area			
Treatments		LU26S		Punjab-85		LU26S		Punjab-85	
NaCl stress	pH	Means	± SE	Means	± SE	Means	± SE	Means	± SE
0 mol m^{-3}	6.0	4.6	0.19	5.0	0.00	4.4	0.23	4.8	0.17
0 mol m^{-3}	8.0	4.6	0.19	5.0	0.00	5.0	0.00	4.9	0.08
100 mol m^{-3}	6.0	1.8	0.11	1.0	0.00	3.4	0.43	1.3	0.18
100 mol m^{-3}	8.0	2.3	0.22	1.3	0.14	4.1	0.37	1.4	0.19
Variety means									
LU26S		3.3				4.3			
Punjab-85		3.1				3.1			
NaCl means									
0 mol m^{-3}		4.8				4.8			
100 mol m^{-3}		1.6				2.6			
pH means									
pH 6.0		3.1				3.5			
pH 8.0		3.3				3.9			
V x S means		0 mol m^{-3} NaCl		100 mol m^{-3} NaCl		0 mol m^{-3} NaCl		100 mol m^{-3} NaCl	
LU26S		4.6		2.1		4.7		3.8	
Punjab-85		5.0		1.2		4.9		1.3	
S x pH means		pH 6.0		pH 8.0					
0 mol m^{-3} NaCl		4.8		4.8					
100 mol m^{-3} NaCl		1.4		1.8					

LSD values at $p = 0.05$

Parameters	V	S	pH	V*S	V*pH	S*pH	V*S*pH
Green leaf area	0.20 *	0.20 ***	0.20 *	0.29 ***	NS	0.29 *	NS
G.flag leaf area	0.35 ***	0.35 ***	0.35 *	0.50 ***	NS	NS	NS

Grading criteria: Grade 1= 0 - 20% green leaf area, Grade 2= 21 - 40% green leaf area
Grade 3= 41 - 60% green leaf area, Grade 4= 61 - 80% green leaf area
Grade 5= 81 -100% green leaf area

- All values (V*S*pH) are means of twelve observations.
- All values for variety, NaCl stress and pH means are averages of 48 observations.

*** = significant at $p<0.001$, * = significant at $p<0.05$

area as compared to salt-sensitive variety Punjab-85. The grading showed that green flag leaf area was comparatively less affected by the salinity than the over all green leaf area.

Variety x salinity interaction were highly significant for both types of leaf area i.e. the decrease in both types of green leaf area at high salinity was greater in Punjab-85 than in LU26S. Salinity x pH interaction was also found to be significant for total green leaf area showing that high pH had no effect on this parameter at 0 mol m^{-3} NaCl stress but a significant increase was noted at 100 mol m^{-3} NaCl salinity.

7.3.3 Ion Composition of Cell Sap at 37 DAS

Na^+ and K^+ contents :

Na^+ and K^+ contents in the cell sap obtained from the 6th leaves are presented in Table - 7.9. There were very large increases in Na^+ and comparatively smaller decreases in K^+ contents as a result of 100 mol m^{-3} NaCl salinity.

Na^+ content was increased significantly by pH 8 at 100 mol m^{-3} NaCl salinity but there was no effect at 0 mol m^{-3} NaCl. Punjab-85 (salt sensitive variety) accumulated more Na^+ than LU26S. Variety x pH interactions were non-significant at both the salinity stresses. This shows that both the varieties behaved similarly at different pH levels. This effect was similar at both the stress levels.

K^+ decreased significantly as a result of 100 mol m^{-3} NaCl salinity but increased significantly at higher pH level. All the interactions were found to be significant except salinity x pH. This shows that high salinity caused a smaller uptake of K^+ in both the varieties as compared to 0 mol m^{-3} NaCl and significantly greater amounts of K^+ was recorded in cell sap of Punjab-85 than LU26S. Variety x pH interactions were also significant which indicates that high pH resulted in a significantly greater K^+ content in the cell sap of LU26S while there was no effect in Punjab-85. The Variety x salinity x pH interaction was also significant at $p<0.05$. This showed that Punjab-85 accumulated greater amounts of K^+ at higher salinity level but lower amounts of K^+ at 0 mol m^{-3} NaCl salinity as compared to the salt tolerant variety LU26S, however the differences were significant only at $S_{100}pH_{6.0}$. The differences between the varieties in K^+ contents were significant only at $S_{100}pH_{6.0}$ and not at other salinity and pH levels.

Table - 7.9: Effect of salinity and pH of the culture solution on Na^+ and K^+ contents (mol m^{-3}) in cell sap of 6th leaves of LU26S and Punjab-85 wheat varieties at 37 DAS.

		Na^+				K^+			
Treatments		LU26S		Punjab-85		LU26S		Punjab-85	
NaCl stress	pH	Means	± SE	Means	± SE	Means	± SE	Means	± SE
0 mol m^{-3}	6.0	3	0.17	3	0.15	210	4.81	197	7.65
0 mol m^{-3}	8.0	3	0.19	4	0.21	231	4.36	214	7.58
100 mol m^{-3}	6.0	238	3.60	250	10.90	121	8.70	197	11.04
100 mol m^{-3}	8.0	258	6.30	273	10.90	161	6.35	181	5.79
Variety means									
LU26S						181			
Punjab-85						197			
NaCl means									
0 mol						213			
100 mol						165			
pH means			100 mol						
pH 6.0			244			181			
pH 8.0			266			197			
V x S means						0 mol m^{-3} NaCl		100 mol m^{-3} NaCl	
LU26S						220		141	
Punjab-85						205		189	
V x pH means						pH 6.0		pH 8.0	
LU26S						166		196	
Punjab-85						197		198	
S x pH means		pH 6.0		pH 8.0					
0 mol m^{-3}NaCl		3		3					
100mol m^{-3}		244		266					

LSD values at $p = 0.05$

Parameters	Variety	pH	Variety x pH
Na^+ (0 mol m^{-3} NaCl)	NS	NS	NS
Na^+ (100 mol m^{-3} NaCl)	NS	16.87 *	NS

Parameters	V	S	pH	V*S	V*pH	S*pH	V*S*pH
K^+	10.5 **	10.5 ***	10.5 **	15.2 ***	15.2 **	NS	22.8 *

- All values (V*S*pH) are means of twelve observations.
- All values for variety, NaCl stress and pH means are averages of 48 observations.

*** = significant at $p<0.001$; ** = significant at $p<0.01$; * = significant at $p<0.05$

Ca^{2+} and Mg^{2+} contents :

Contents of Mg^{2+} in the 6th leaves were higher than Ca^{2+} contents (Table 7.10). There was a significant decrease in Ca^{2+} contents of the leaves as a result of 100 mol m^{-3} NaCl salinity. Effect of variety was highly significant and Ca^{2+} contents were greater in the salt tolerant variety LU26S. A decrease in Ca^{2+} contents was also observed at higher pH level although the effect was non-significant. Variety x salinity and salinity x pH interactions were found to be significant while other interactions were non-significant. Decreases in Ca^{2+} contents at higher salinity were greater in Punjab-85 than LU26S. Also, high pH resulted in a decrease in Ca^{2+} contents at 0 mol m^{-3} NaCl salinity while there was an increase at 100 mol m^{-3} NaCl salinity.

Mg^{2+} contents were also decreased significantly as a result of 100 mol m^{-3} NaCl salinity (Table 7.10). The leaves of salt tolerant variety LU26S had a significantly higher Mg^{2+} content than leaves of salt sensitive variety Punjab-85. The effects of pH and all the interactions were non-significant.

Cl^- contents :

There was a large and significant increase in Cl^- contents as a result of 100 mol m^{-3} NaCl salinity in both the varieties (Table 7.11). A significant increase was also observed due to a higher pH level. The salt sensitive variety Punjab-85, contained slightly higher amounts of Cl^- as compared to the salt tolerant variety LU26S , the differences however were non-significant. All the interactions were found to be non-significant.

K^+/Na^+ ratio :

The K^+/Na^+ ratios were markedly lower at 100 mol m^{-3} NaCl salinity (Table 7.11) than 0 mol m^{-3} NaCl salinity. These ratios were significantly greater in the salt-tolerant variety LU26S as compared to the salt-sensitive variety Punjab-85 at both the stress levels. The effects of pH were non-significant at both the salinity levels. Variety x pH interaction was significant at 100 mol m^{-3} NaCl which showed that K^+/Na^+ ratio was decreased by pH 8 in Punjab-85 but was increased in LU26S. The same interaction was found to be non-significant at 0 mol m^{-3} NaCl stress.

Table - 7.10: Effect of salinity and pH of the culture solution on Ca^{2+} and Mg^{2+} (mol m^{-3}) in cell sap of 6th leaves of LU26S and Punjab-85 wheat varieties at 37 DAS.

		Ca^{2+}				Mg^{2+}			
Treatments		LU26S		Punjab-85		LU26S		Punjab-85	
NaCl stress	pH	Means	± SE	Means	± SE	Means	± SE	Means	± SE
0 mol m^{-3}	6.0	5.10	0.26	3.96	0.14	20.4	1.56	18.0	0.94
0 mol m^{-3}	8.0	4.56	0.26	3.81	0.14	21.2	1.74	16.1	1.36
100 mol m^{-3}	6.0	1.18	0.08	0.85	0.04	11.4	0.95	7.6	0.89
100 mol m^{-3}	8.0	1.40	0.10	0.89	0.06	11.8	0.76	7.6	0.77
Variety means									
LU26S		3.06				16.2			
Punjab-85		2.38				12.3			
NaCl means									
0 mol m^{-3}		4.36				18.9			
100 mol m^{-3}		1.08				9.6			
V x S means		0 mol m^{-3} NaCl		100 mol m^{-3} NaCl					
LU26S		4.83		1.29					
Punjab-85		3.89		0.87					
S x pH means		pH 6		pH 8					
0 mol m^{-3} NaCl		4.53		4.19					
100 mol m^{-3} NaCl		1.02		1.46					

LSD values at $p = 0.05$

Parameters	V	S	pH	V*S	V*pH	S*pH	V*S*pH
Ca^{2+}	0.22 ***	0.22 ***	NS	0.32 *	NS	0.32 *	NS
Mg^{2+}	1.67 ***	1.67 ***	NS	NS	NS	NS	NS

- All values (V*S*pH) are means of twelve observations.
- All values for variety, NaCl stress and pH means are averages of 48 observations.

*** = significant at $p<0.001$

* = significant at $p<0.05$

Table - 7.11: Effect of salinity and pH of the culture solution on chlorides (mol m^{-3}) and K^+/Na^+ ratio of cell sap in leaves of LU26S and Punjab-85 wheat varieties at 37 DAS.

		Cl^-				K^+/Na^+			
Treatments		LU26S		Punjab-85		LU26S		Punjab-85	
NaCl stress	pH	Means	± SE	Means	± SE	Means	± SE	Means	± SE
0 mol m^{-3}	6.0	31	1.5	38	1.95	66.6	4.29	61.3	3.33
0 mol m^{-3}	8.0	35	1.2	44	2.49	77.5	6.28	61.3	4.18
100 mol m^{-3}	6.0	253	7.1	271	15.2	0.5	0.04	0.8	0.09
100 mol m^{-3}	8.0	283	4.2	292	12.2	0.6	0.02	0.7	0.04
Variety means						0 mol	100 mol		
LU26S						3.2	248		
Punjab-85						3.5	262		
NaCl means									
0 mol m^{-3}		37							
100 mol m^{-3}		275							
pH means									
pH 6.0		148							
pH 8.0		164							
V x pH means						pH 6		pH 8	
LU26S						0.52		0.63	
Punjab-85						0.82		0.68	

LSD values at $p = 0.05$

Parameters	V	S	pH	V*S	V*pH	S*pH	V*S*pH
Cl^-	NS	10.8 ***	10.8 **	NS	NS	NS	NS

Parameters	Variety	pH	Variety x pH
K^+/Na^+ (0 mol m^{-3} NaCl)	9.20 *	NS	NS
K^+/Na^+ (100 mol m^{-3} NaCl)	0.11 **	NS	0.15 *

- All values (V*S*pH) are means of twelve observations.
- All values for variety, NaCl stress and pH means are averages of 48 observations.

*** = significant at $p<0.001$, ** = significant at $p<0.01$, * = significant at $p<0.05$

7.3.4 Ion Contents in Dry Plant Material at 38 DAS

Na^+ and K^+ contents :

Na^+ contents in the dry matter at 38 DAS are presented in Table 7.12. There was a considerable increase in Na^+ at 100 mol m^{-3} NaCl salinity. An increase was also noted at higher pH level. Salt-sensitive variety Punjab-85 contained significantly greater amounts of Na^+ than the salt-tolerant variety LU26S at both the salinity levels. There was no significant effect of high pH at S_0 but at S_{100} the effect was significant and about 11% higher Na^+ was noted.

K^+ contents in the dry matter at 38 DAS are presented in Table 7.12. There was a significant decrease in K^+ contents caused by 100 mol m^{-3} NaCl salinity. A notable increase was noted in K^+ contents at higher pH level and 100 mol m^{-3} NaCl in both the varieties. Differences in between the varieties for K^+ contents were non-significant. All the interactions were non-significant in this case.

Ca^{2+} and Mg^{2+} contents :

Ca^{2+} and Mg^{2+} contents in the dry plant material are presented in Table 7.13. Ca^{2+} content was significantly decreased by 100 mol m^{-3} NaCl salinity and higher pH. LU26S had significantly higher Ca^{2+} than the salt sensitive variety Punjab-85. All the interactions were non-significant except variety x salinity and variety x salinity x pH. A significant variety x salinity interaction showed that the decrease in Ca^{2+} at 100 mol m^{-3} NaCl was smaller in the salt-sensitive variety Punjab-85 than the salt-tolerant variety LU26S. Also, at low salinity LU26S had significantly higher Ca^{2+} contents while at 100 mol m^{-3} NaCl, the differences were non-significant.

A significant variety x salinity x pH interaction indicated that Ca^{2+} was decreased significantly in LU26S as a result of higher salinity and higher pH level. In Punjab-85 also, Ca^{2+} decreased in $S_0pH_{8.0}$ as compared to $S_0pH_{6.0}$ and also in $S_{100}pH_{8.0}$ than $S_{100}pH_{6.0}$ but the differences were non-significant. The differences between the varieties were significant only at $S_0pH_{6.0}$; where significantly higher Ca^{2+} contents were noted in the salt-tolerant variety LU26S than the salt-sensitive variety Punjab-85.

Mg^{2+} was also significantly decreased at 100 mol m^{-3} salinity in the nutrient solution but there was no effect of higher pH. LU26S had significantly higher contents of Mg^{2+}. Variety x pH was significant while all the other interactions were non-significant. A significant variety x pH interaction showed that there was a non-significant decrease in Mg^{2+} contents at high pH in LU26S but conversely, there was a significant increase in Punjab-85.

Table - 7.12: Effect of salinity and pH of the culture solution on Na^+ and K^+ contents (mg g^{-1} dry weight) in dry matter of LU26S and Punjab-85 wheat varieties at 38 DAS.

		Na^+				K^+			
Treatments		LU26S		Punjab-85		LU26S		Punjab-85	
NaCl stress	pH	Means	± SE	Means	± SE	Means	± SE	Means	± SE
0 mol m^{-3}	6.0	2.0	0.14	2.5	0.23	56.9	0.84	56.6	1.19
0 mol m^{-3}	8.0	2.1	0.18	2.8	0.46	57.9	0.58	58.9	1.12
100 mol m^{-3}	6.0	26.5	0.80	28.1	0.95	37.1	0.63	36.3	0.62
100 mol m^{-3}	8.0	28.0	1.25	32.9	1.92	40.3	2.49	40.6	1.32
Variety means		0 mol	100 mol						
LU26S		2.0	27.3			48.0			
Punjab-85		2.6	30.4			48.1			
NaCl means									
0 mol m^{-3}						57.6			
100 mol m^{-3}						38.6			
pH means		100 mol							
pH 6.0		27.3				46.8			
pH 8.0		30.4				49.4			
S x pH means		pH 6.0		pH 8.0					
0 mol m^{-3} NaCl		2.3		2.4					
100 mol m^{-3} NaCl		27.3		30.4					

LSD values at $p = 0.05$

Parameter	Variety	pH	Variety x pH
Na^+ (0 mol m^{-3} NaCl)	0.56 *	NS	NS
Na^+ (100 mol m^{-3} NaCl)	2.58 *	2.58 *	NS

Parameter	V	S	pH	V*S	V*pH	S*pH	V*S*pH
K^+	NS	1.77 ***	1.77 *	NS	NS	NS	NS

- All values (V*S*pH) are means of twelve observations.
- All values for variety, NaCl stress and pH means are averages of 48 observations.

*** = significant at $p<0.001$

** = significant at $p<0.01$

* = significant at $p<0.05$

Table - 7.13: Effect of salinity and pH of the culture solution on Ca^{2+} and Mg^{2+} contents (mg g^{-1} dry weight) in dry matter of LU26S and Punjab-85 wheat varieties at 38 DAS.

		Ca^{2+}				Mg^{2+}			
Treatments		LU26S		Punjab-85		LU26S		Punjab-85	
NaCl stress	pH	Means	± SE	Means	± SE	Means	± SE	Means	± SE
0 mol m^{-3}	6.0	0.62	0.02	0.52	0.01	2.17	0.05	1.80	0.07
0 mol m^{-3}	8.0	0.50	0.01	0.48	0.01	2.04	0.52	1.97	0.08
100 mol m^{-3}	6.0	0.30	0.01	0.32	0.03	1.69	0.07	1.49	0.09
100 mol m^{-3}	8.0	0.28	0.01	0.27	0.01	1.54	0.09	1.64	0.05
Variety means									
LU26S		0.42				1.86			
Punjab-85		0.40				1.73			
NaCl means									
0 mol m^{-3}		0.53				1.99			
100 mol m^{-3}		0.29				1.59			
pH means									
pH 6.0		0.44				1.79			
pH 8.0		0.38				1.79			
V x S means		0 mol m^{-3} NaCl		100 mol m^{-3} NaCl		0 mol m^{-3} NaCl		100 mol m^{-3} NaCl	
LU26S		0.56		0.29		-		-	
Punjab-85		0.49		0.29		-		-	
V x pH means		pH 6		pH 8		pH 6		pH 8	
LU26S		-		-		1.93		1.79	
Punjab-85		-		-		1.65		1.80	

LSD values at p = 0.05

Parameters	V	S	pH	V*S	V*pH	S*pH	V*S*pH
Ca^{2+}	0.02 *	0.02 ***	0.02 ***	0.03 **	NS	NS	0.05 *
Mg^{2+}	0.10 *	0.10 ***	NS	NS	0.15 **	NS	NS

- All values (V*S*pH) are means of twelve observations.
- All values for variety, NaCl stress and pH means are averages of 48 observations.

*** = significant at $p<0.001$; ** = significant at $p<0.01$

* = significant at $p<0.05$

Cl^- contents :

Cl^- contents of the dry matter are presented in Table 7.14. There was a highly significant increase in the Cl^- contents as a result of 100 mol m^{-3} NaCl salinity as compared to 0 mol m^{-3} NaCl salinity but there was no effect of high pH or the variety. All the interactions were found to be non-significant.

K^+/Na^+ ratio :

K^+/Na^+ ratio was significantly greater in the salt-tolerant variety LU26S than in the salt-sensitive variety Punjab-85 at 0 mol m^{-3} salinity level but at 100 mol m^{-3} salinity, the differences between the varieties were non-significant (Table 7.14). There was a considerable decrease in K^+/Na^+ ratio brought about by 100 mol m^{-3} NaCl salinity in both the varieties. Effect of high pH on K^+/Na^+ ratio was not clear.

Zinc (Zn^{2+}) contents :

Zn^{2+} contents in the dry matter were significantly decreased at 100 mol m^{-3} NaCl salinity and higher pH level (Table 7.15). However the varieties did not differ in their zinc contents. All the interactions were non-significant except variety x salinity x pH interaction. This showed that Zn^{2+} contents decreased significantly in both the varieties at higher salinity level and higher pH level. In both the varieties, Zn^{2+} contents were significantly similar in $S_0pH_{6.0}$ but in $S_0pH_{8.0}$ Zn^{2+} contents in LU26S were significantly higher than Punjab-85. Differences in between the varieties in $S_{100}pH_{6.0}$ and $S_{100}pH_{8.0}$ were non-significant.

Iron (Fe^{2+}) contents :

Table 7.15 shows the effect of different salinity and pH levels on the Fe^{2+} contents of the dry matter. Iron contents were significantly decreased at 100 mol m^{-3} NaCl salinity and the salt sensitive variety Punjab-85 had significantly higher iron contents. Decrease in iron contents due to higher pH was about 8% but was non-significant. The variety x salinity interaction was significant while all the other interactions were non-significant. A significant variety x salinity interaction showed that decrease in Fe^{2+} contents at high salinity was greater in LU26S than in

Table - 7.14: Effect of salinity and pH of the culture solution on chloride contents (mg g^{-1} dry weight) and K^+/Na^+ ratio in dry matter of LU26S and Punjab-85 wheat varieties at 38 DAS.

		Cl^-				K^+/Na^+			
Treatments		LU26S		Punjab-85		LU26S		Punjab-85	
NaCl stress	pH	Means	± SE	Means	± SE	Means	± SE	Means	± SE
0 mol m^{-3}	6.0	2.5	0.11	2.7	0.09	31.7	5.14	23.9	1.41
0 mol m^{-3}	8.0	2.1	0.11	2.6	0.06	30.4	2.61	24.1	2.00
100 mol m^{-3}	6.0	13.9	0.49	15.3	0.56	1.4	0.03	1.3	0.04
100 mol m^{-3}	8.0	14.6	0.37	14.3	0.60	1.5	0.12	1.3	0.09
Variety means						0 mol m^{-3} NaCl			
LU26S						31.1			
Punjab-85						24.0			
NaCl means									
0 mol m^{-3}		2.5				27.5			
100 mol m^{-3}		14.5				1.4			

LSD values at $p = 0.05$

Parameter	V	S	pH	V*S	V*pH	S*pH	V*S*pH
Cl^-	NS	0.52 ***	NS	NS	NS	NS	NS

Parameters	Variety	pH	Variety x pH
K^+/Na^+ ratio (0 mol m^{-3} NaCl)	6.20 *	NS	NS
K^+/Na^+ ratio (100 mol m^{-3} NaCl)	NS	NS	NS

- All values (V*S*pH) are means of twelve observations.
- All values for variety, NaCl stress and pH means are averages of 48 observations.

*** = significant at $p<0.001$

* = significant at $p<0.05$

Table - 7.15: Effect of salinity and pH of the culture solution on zinc and iron contents ($\mu g\ g^{-1}$ dry weight) in dry matter of LU26S and Punjab-85 wheat varieties at 38 DAS.

Treatments		Zinc				Iron			
		LU26S		Punjab-85		LU26S		Punjab-85	
NaCl stress	pH	Means	± SE	Means	± SE	Means	± SE	Means	± SE
0 mol m^{-3}	6.0	64.8	1.91	64.8	3.80	156	5.75	144	10.90
0 mol m^{-3}	8.0	51.1	1.85	42.8	1.12	139	10.40	142	7.27
100 mol m^{-3}	6.0	55.9	2.35	51.5	3.03	126	9.20	151	8.51
100 mol m^{-3}	8.0	37.2	0.97	39.8	2.21	107	4.44	142	7.86
Variety means									
LU26S		52.3				132			
Punjab-85		49.7				145			
NaCl means									
0 mol m^{-3}		55.8				145			
100 mol m^{-3}		46.1				132			
pH means									
pH 6.0		59.2				144			
pH 8.0		42.7				133			
V x S means		0 mol m^{-3} NaCl		100 mol m^{-3} NaCl		0 mol m^{-3} NaCl		100 mol m^{-3} NaCl	
LU26S		-		-		148		117	
Punjab-85		-		-		143		146	

LSD values at p = 0.05

Parameters	V	S	pH	V*S	V*pH	S*pH	V*S*pH
Zinc	NS	3.29 ***	3.29 ***	NS	NS	NS	7.15 *
Iron	11.8 *	11.8 *	NS	16.6 **	NS	NS	NS

- All values (V*S*pH) are means of twelve observations.
- All values for variety, NaCl stress and pH means are averages of 48 observations.

*** = significant at p<0.001

** = significant at p<0.01

* = significant at p<0.05

Punjab-85 where a slight non-significant increase was noted. At low salinity level, there were no significant differences in Fe^{2+} contents of the varieties.

Manganese (Mn^{2+}) contents :

LU26S had significantly higher manganese (Mn^{2+}) contents in the dry matter than the salt sensitive variety Punjab-85 (Table 7.16). There were highly significant effects of salinity and pH on Mn^{2+} contents which decreased considerably at higher levels of NaCl salinity and pH. All the interactions were found to be non-significant except salinity x pH interaction which was highly significant ($p<0.001$). This indicated that high pH resulted in a significant decrease in Mn^{2+} contents at 0 mol m^{-3} NaCl but at 100 mol m^{-3} NaCl salinity, a non-significant increase was noted at higher pH.

7.3.5 Final Yield Data

Number of tillers and ears per plant :

Data for number of tillers (including the main stem) and number of ears per plant recorded at the time of final harvest is presented in Table 7.17. Number of tillers was significantly higher in salt-sensitive variety Punjab-85 and there was significant decrease in the number of tillers at 100 mol m^{-3} NaCl stress. Effect of pH was not significant. Variety x salinity interaction was highly significant while all the other interactions were non-significant. Although at 0 mol m^{-3} salinity, Punjab-85 had more total number of tillers per plant but the decrease due to 100 mol m^{-3} NaCl salinity in LU26S was smaller (about 50%) as compared to the salt-sensitive variety Punjab-85 (62%), so that at 100 mol m^{-3} NaCl, they had similar numbers of tillers.

Number of ears per plant was decreased significantly by 100 mol m^{-3} NaCl salinity while the effects of varieties, pH and all the interactions were non-significant. Number of ears per plant was also higher in Punjab-85 than LU26S and also was higher at pH 8.0 but the differences were not significant.

Total number of spikelets and fertile spikelets/ear :

Total number of spikelets per ear (Table 7.18) was significantly decreased by the higher level of salinity and differences between the varieties were also highly significant. Effect of pH

Table - 7.16: Effect of salinity and pH of the culture solution on manganese (Mn^{2+}) contents ($\mu g\ g^{-1}$ dry weight) in dry matter of LU26S and Punjab-85 wheat varieties at 38 DAS.

		Manganese			
Treatments		LU26S		Punjab-85	
NaCl stress	pH	Means	± SE	Means	± SE
0 mol m^{-3}	6.0	143	3.76	133	6.72
0 mol m^{-3}	8.0	119	2.37	104	2.96
100 mol m^{-3}	6.0	87	1.89	68	3.58
100 mol m^{-3}	8.0	97	4.56	73	2.73
Variety means					
LU26S		112			
Punjab-85		94			
NaCl means					
0 mol m^{-3}		125			
100 mol m^{-3}		81			
pH means					
pH 6.0		108			
pH 8.0		98			
S x pH means		pH 6		pH 8	
0 mol m^{-3} NaCl		138		112	
100 mol m^{-3} NaCl		78		85	

LSD values at p = 0.05

Parameters	V	S	pH	V*S	V*pH	S*pH	V*S*pH
Mn	5.47 ***	5.47 ***	5.47 ***	NS	NS	7.92 ***	NS

- All values (V*S*pH) are means of twelve observations.
- All values for variety, NaCl stress and pH means are averages of 48 observations.

*** = significant at p<0.001

Table - 7.17: Effect of salinity and pH of the culture solution on number of tillers (including main stem) and number of ears per plant in LU26S and Punjab-85 wheat varieties at final harvest.

		Number of tillers/plant				Number of ears/plant			
Treatments		LU26S		Punjab-85		LU26S		Punjab-85	
NaCl stress	pH	Means	± SE	Means	± SE	Means	± SE	Means	± SE
0 mol m^{-3}	6.0	6.0	0.34	8.8	0.76	6.0	0.34	7.4	0.68
0 mol m^{-3}	8.0	7.4	0.59	8.6	0.62	7.3	0.59	7.3	0.56
100 mol m^{-3}	6.0	3.4	0.16	3.6	0.12	3.2	0.12	3.0	0.08
100 mol m^{-3}	8.0	3.3	0.11	3.1	0.15	3.2	0.10	2.7	0.14
Variety means									
LU26S		5.0				4.9			
Punjab-85		6.0				5.1			
NaCl means									
0 mol m^{-3}		7.7				7.0			
100 mol m^{-3}		3.3				3.0			
V x S means		0 mol m^{-3} NaCl		100 mol m^{-3} NaCl					
LU26S		6.7		3.4					
Punjab-85		8.7		3.3					

LSD values at $p = 0.05$

Parameters	V	S	pH	V*S	V*pH	S*pH	V*S*pH
Number of tillers	0.61 **	0.61 ***	NS	0.87 ***	NS	NS	NS
Number of ears	NS	0.57 ***	NS	NS	NS	NS	NS

- All values (V*S*pH) are means of eighteen observations.
- All values for variety, NaCl stress and pH means are averages of 72 observations.

*** = significant at $p<0.001$
** = significant at $p<0.01$

Table - 7.18: Effect of salinity and pH of the culture solution on total number of spikelets and fertile spikelets per ear in LU26S and Punjab-85 wheat varieties at final harvest.

		Total number of spikelets/ear				Fertile spikelets/ear			
Treatments		LU26S		Punjab-85		LU26S		Punjab-85	
NaCl stress	pH	Means	± SE	Means	± SE	Means	± SE	Means	± SE
0 mol m^{-3}	6.0	15.5	0.35	16.6	0.30	10.6	0.41	12.9	0.49
0 mol m^{-3}	8.0	15.4	0.29	16.2	0.25	10.8	0.31	12.1	0.33
100 mol m^{-3}	6.0	14.9	0.23	15.7	0.22	6.1	0.24	8.0	0.26
100 mol m^{-3}	8.0	14.8	0.18	15.7	0.26	6.5	0.25	7.2	0.27
Variety means									
LU26S		15.2				8.5			
Punjab-85		16.1				10.4			
NaCl means									
0 mol m^{-3}		15.9				11.6			
100 mol m^{-3}		15.3				6.9			
V x pH means						pH 6		pH 8	
LU26S						8.3		8.6	
Punjab-85						10.4		9.6	

LSD values at p = 0.05

Parameters	V	S	pH	V*S	V*pH	S*pH	V*S*pH
Total spikelets/ear	0.37 ***	0.37 ***	NS	NS	NS	NS	NS
Fertile spikelets/ear	0.46 ***	0.65 ***	NS	NS	0.65 *	NS	NS

- All values (V*S*pH) are means of eighteen observations.
- All values for variety, NaCl stress and pH means are averages of 72 observations.

*** = significant at $p<0.001$
** = significant at $p<0.01$
* = significant at $p<0.05$

levels and all the interactions were non-significant.

Number of fertile spikelets per ear was decreased significantly by 100 mol m^{-3} NaCl stress and was significantly higher in Punjab-85 than LU26S (Table 7.18). The fertile spikelets per ear were also slightly higher at lower pH level but the effect was non-significant. Variety x pH interaction was significant while other interactions were not significant. This showed that at higher pH level, LU26S had slightly higher number of fertile spikelets per ear while a decrease occurred in Punjab-85.

Infertile (sterile) spikelets per ear and fertile : infertile ratio :

Number of infertile/sterile spikelets per ear (Table 7.19) was significantly higher in LU26S and was significantly greater at 100 mol m^{-3} NaCl salinity level as compared to 0 mol m^{-3} salinity. All the interactions were non-significant except variety x pH. This indicated that at pH 6.0 the sterile spikelets were more in LU26S but there were no significant differences between the varieties at pH 8.0.

Fertile:infertile spikelet ratio (Table 7.19) was significantly higher in salt sensitive variety Punjab-85 and was significantly decreased by 100 mol m^{-3} NaCl salinity. Higher pH had a non-significant effect. Effect of variety x salinity and variety x pH was also significant. This showed that the ratio was higher in Punjab-85 than LU26S at lower level of salinity and pH but the differences at higher level of salinity and pH were non-significant.

Length of main stems:

Length of main stems at final harvest (Table 7.20) was significantly higher in the salt tolerant variety LU26S and was significantly decreased by 100 mol m^{-3} NaCl salinity but the effect of pH was not significant. Except variety x salinity x pH interaction, all the interactions were found to be significant. Decrease in the length of main stems as a result of 100 mol m^{-3} NaCl salinity was greater in the salt-sensitive variety Punjab-85 than the salt-tolerant variety LU26S . At higher pH, length of main stems was increased in LU26S but was decreased in Punjab-85. Higher pH caused an increase in the length of the main stems at 0 mol m^{-3} salinity but a significant decrease was noted at 100 mol m^{-3} NaCl.

Table - 7.19: Effect of salinity and pH of the culture solution on infertile (sterile) spikelets per ear and fertile spikelet : infertile spikelet ratio in LU26S and Punjab-85 wheat varieties at final harvest.

		Infertile spikelets/ear				Fertile:infertile spikelets			
Treatments		LU26S		Punjab-85		LU26S		Punjab-85	
NaCl stress	pH	Means	± SE	Means	± SE	Means	± SE	Means	± SE
0 mol m^{-3}	6.0	4.96	0.43	3.72	0.36	2.44	0.23	4.34	0.62
0 mol m^{-3}	8.0	4.55	0.42	4.06	0.31	2.70	0.23	3.35	0.32
100 mol m^{-3}	6.0	8.80	0.25	7.69	0.25	0.71	0.04	1.07	0.06
100 mol m^{-3}	8.0	8.38	0.27	8.56	0.32	0.80	0.06	0.87	0.05
Variety means									
LU26S		6.67				1.66			
Punjab-85		6.01				2.41			
NaCl means									
0 mol m^{-3}		4.32				3.21			
100 mol m^{-3}		8.36				0.86			
V x S means		0 mol m^{-3} NaCl		100 mol m^{-3} NaCl		0 mol m^{-3} NaCl		100 mol m^{-3} NaCl	
LU26S		-		-		2.57		0.76	
Punjab-85		-		-		3.85		0.97	
V x pH means		pH 6		pH 8		pH 6		pH 8	
LU26S		29.3		30.6		1.57		1.75	
Punjab-85		25.4		26.1		2.70		2.11	

LSD values at $p = 0.05$

Parameters	V	S	pH	V*S	V*pH	S*pH	V*S*pH
Infertile spikelets/ear	0.47 ***	0.47 ***	NS	NS	0.66 *	NS	NS
Fertile:infertile spikelet	0.38 ***	0.38 ***	NS	0.54 **	0.54 *	NS	NS

- All values (V*S*pH) are means of eighteen observations.
- All values for variety, NaCl stress and pH means are averages of 72 observations.

*** = significant at $p<0.001$, ** = significant at $p<0.01$

* = significant at $p<0.05$

Table - 7.20: Effect of salinity and pH of the culture solution on length of main stem (cm) and dry weight/plant (g) in LU26S and Punjab-85 wheat varieties at final harvest.

		Length of main stem				Dry weight/plant			
Treatments		LU26S		Punjab-85		LU26S		Punjab-85	
NaCl stress	pH	Means	± SE	Means	± SE	Means	± SE	Means	± SE
0 mol m^{-3}	6.0	81.5	1.19	73.5	1.24	9.81	0.74	12.08	0.90
0 mol m^{-3}	8.0	85.0	0.80	73.6	0.87	11.80	0.75	11.23	0.74
100 mol m^{-3}	6.0	63.9	0.87	52.8	1.01	2.94	0.14	2.31	0.13
100 mol m^{-3}	8.0	63.7	1.37	46.5	0.62	3.16	0.17	1.73	0.07
Variety means									
LU26S		73.3				6.93			
Punjab-85		61.6				6.84			
NaCl means									
0 mol m^{-3}		78.4				11.2			
100 mol m^{-3}		56.7				2.54			
V x S means		0 mol m^{-3} NaCl		100 mol m^{-3} NaCl		0 mol m^{-3} NaCl		100 mol m^{-3} NaCl	
LU26S		83		64		11.81		3.05	
Punjab-85		74		50		11.66		2.03	
V x pH means		pH 6		pH 8		pH 6		pH 8	
LU26S		73		74		6.38		7.48	
Punjab-85		63		60		7.19		6.49	
S x pH means		pH 6		pH 8					
0 mol m^{-3} NaCl		78		79					
100 mol m^{-3} NaCl		58		55					

LSD values at p = 0.05

Parameters	V	S	pH	V*S	V*pH	S*pH	V*S*pH
Length of m. stem	1.44 ***	1.44 ***	NS	2.08 **	2.08 **	2.08 **	NS
Weight (g)/plant	NS	0.79 ***	NS	1.15 **	1.15 *	NS	NS

- All values (V*S*pH) are means of eighteen observations.
- All values for variety, NaCl stress and pH means are averages of 72 observations.

*** = significant at $p<0.001$; ** = significant at $p<0.01$; * = significant at $p<0.05$

Dry weight per plant (grain + straw) :

The effect of NaCl salinity on dry weight per plant was highly significant while it was non-significant for variety and pH at final harvest (Table 7.20). All the interactions were non-significant except variety x salinity and variety x pH interactions. A significant variety x salinity interaction showed that decrease in dry weight was higher in the salt-sensitive variety Punjab-85 (91%) than the salt-tolerant variety LU26S (72%). At higher pH level, dry weight increased in LU26S but decreased in the salt-sensitive variety Punjab-85.

Number of grains and weight of grains per plant :

The data for number of grains and weight of grains per plant are presented in Table 7.21. Number of grains per plant was significantly lower in LU26S and at 100 mol m^{-3} NaCl salinity. The effects of pH and all the interactions were non-significant except variety x salinity. This shows that at 0 mol m^{-3} salinity, number of grains was significantly higher in Punjab-85 while at 100 mol m^{-3} NaCl salinity, the differences were non-significant. Percentage decrease in the number of grains per plant due to higher salinity was greater in the salt-sensitive variety Punjab-85 (81%) than LU26S (74%).

The effect of variety and pH on the weight of grains per plant was non-significant while the effect of salinity was highly significant (Table 7.21). Variety x salinity interaction was significant ($p<0.01$) which indicated that varieties behaved differently at the two salinity levels. At 0 mol m^{-3} salinity, weight of grains was significantly higher in the salt-sensitive variety Punjab-85 while at 100 mol m^{-3} salinity, grain weight was higher in the salt-tolerant variety LU26S. The decrease due to higher salinity was greater in Punjab-85 (90%) than the salt-tolerant variety LU26S (79%). All the other interactions were non-significant.

The significant varietal differences for number of grains per plant but non-significant varietal differences for weight of grains showed that the grains in salt sensitive variety Punjab-85 were of much smaller size.

Hundred grain weight :

Hundred grain weight was significantly different in both the varieties and at both the salinity levels, the effect of pH being non-significant (Table 7.22). Variety x salinity interaction was significant showing that decreases in 100 grain weight were greater in the salt-sensitive

Table - 7.21: Effect of salinity and pH of the culture solution on total number of grains and weight of grains per plant (g) in LU26S and Punjab-85 wheat varieties at final harvest.

		Total number grains/plant				Weight of grains/plant			
Treatments		LU26S		Punjab-85		LU26S		Punjab-85	
NaCl stress	pH	Means	± SE	Means	± SE	Means	± SE	Means	± SE
0 mol m^{-3}	6.0	112	10.6	185	17.2	3.85	0.37	5.25	0.37
0 mol m^{-3}	8.0	141	11.3	172	14.1	4.50	0.37	4.85	0.35
100 mol m^{-3}	6.0	32	1.16	38	2.25	0.84	0.06	0.58	0.05
100 mol m^{-3}	8.0	33	1.68	29	1.54	0.91	0.09	0.38	0.01
Variety means									
LU26S		79.3				-			
Punjab-85		106.0				-			
NaCl means									
0 mol m^{-3}		153				4.61			
100 mol m^{-3}		32.9				0.68			
V x S means		0 mol m^{-3} NaCl		100 mol m^{-3} NaCl		0 mol m^{-3} NaCl		100 mol m^{-3} NaCl	
LU26S		126		32		4.17		0.88	
Punjab-85		179		33		5.05		0.48	

LSD values at p = 0.05

Parameters	V	S	pH	V*S	V*pH	S*pH	V*S*pH
No. of grains	13.6 ***	13.6 ***	NS	19.6 ***	NS	NS	NS
Weight of grains(g)	NS	0.37 ***	NS	0.53 **	NS	NS	NS

- All values (V*S*pH) are means of eighteen observations.
- All values for variety, NaCl stress and pH means are averages of 72 observations.

*** = significant at $p<0.001$

** = significant at $p<0.01$

Table - 7.22: Effect of salinity and pH of the culture solution on 100 grain weight (g) and harvest index (%) in LU26S and Punjab-85 wheat varieties at final harvest.

		100 grain weight				Harvest index			
Treatments		LU26S		Punjab-85		LU26S		Punjab-85	
NaCl stress	pH	Means	± SE	Means	± SE	Means	± SE	Means	± SE
0 mol m^{-3}	6.0	3.44	0.12	2.92	0.07	38.3	1.55	43.8	0.94
0 mol m^{-3}	8.0	3.25	0.12	2.87	0.08	38.1	1.64	43.2	0.91
100 mol m^{-3}	6.0	2.65	0.16	1.54	0.10	28.2	1.15	24.9	1.14
100 mol m^{-3}	8.0	2.73	0.17	1.38	0.08	28.6	1.74	22.2	0.80
Variety means									
LU26S		3.02				33.3			
Punjab-85		2.18				33.5			
NaCl means									
0 mol m^{-3}		3.12				40.8			
100 mol m^{-3}		2.07				26.0			
V x S means		0 mol m^{-3} NaCl		100 mol m^{-3} NaCl		0 mol m^{-3} NaCl		100 mol m^{-3} NaCl	
LU26S		3.34		2.69		38.2		28.4	
Punjab-85		2.90		1.46		43.5		23.6	

LSD values at $p = 0.05$

Parameters	V	S	pH	V*S	V*pH	S*pH	V*S*pH
100 grain weight	0.16 ***	0.16 ***	NS	0.24 ***	NS	NS	NS
Harvest index (%)	NS	1.79 ***	NS	2.53 ***	NS	NS	NS

- All values (V*S*pH) are means of eighteen observations.
- All values for variety, NaCl stress and pH means are averages of 72 observations.

*** = significant at $p<0.001$

variety Punjab-85 (50%) than the salt-tolerant variety LU26S (20%). It was also evident that 100 grain weight at 0 mol m^{-3} salinity level was significantly lower in Punjab-85 than LU26S. All the other interactions were non-significant.

Significantly lower 100 grain weight in the salt sensitive variety Punjab-85, showed that at higher salinity level, there was comparatively more hinderance for assimilate transfer to the grains in this variety.

Harvest Index :

Harvest Index ((grain weight/grain+straw weight) x 100) is presented in Table 7.22. Effect of salinity was highly significant while that of varieties and pH was non-significant. All the interactions were non-significant except variety x salinity interaction. At 0 mol m^{-3} salinity, Punjab-85 (salt-sensitive variety) had higher harvest index, while at 100 mol m^{-3} NaCl salinity, it had significantly lower harvest index as compared to salt-tolerant variety LU26S. The decrease in the harvest index caused by 100 mol m^{-3} NaCl salinity over 0 mol m^{-3} salinity was greater in Punjab-85 (47%) than LU26S (26%).

7.4 DISCUSSION

Precipitation of salts in the nutrient solution was negligible in this study. pH of the nutrient solutions kept at high pH were to be maintained daily due to drop in pH as described in Chapter 6 (section 6.1). To avoid excessive build up of K^+ due to use of KOH for raising pH, and any deficiency of nutrients (Guest and Chapman, 1944; Salisbury and Ross, 1991), nutrient solution were changed after every week as was done by Leidi *et al.* (1991a) and in Chapter 6. In spite of this, interveinal chlorosis on some younger leaves was noted in the plants kept at pH 8.0 which is an early symptom of iron deficiency (Salisbury and Ross, 1991). Although manganese deficiency is not common, its symptoms also resemble to those reported above for iron. Wheat and barley are reported to suffer a reduction in growth at pH 8.5 and 9.0 respectively (Hewitt, 1966). In spite of the fact that Fe-EDDHA was used as source for Fe^{2+} which has a better availability under alkaline conditions (Nabhan *et al.* 1977; Chaney, 1988), and the higher pH level was kept at 8.0, the plants in this treatment showed some chlorosis. This paleness and slight chlorosis of leaves could be due to a decrease in chlorophyll concentration in the leaves of wheat with increase in pH of the culture medium as reported by Leidi *et al.* (1991a). Pale colour of the leaves could also be due to disturbance in nitrogen nutrition at high pH (Leidi *et al.* 1991b).

High NaCl salinity and high pH of the nutrient solution affected various gas exchange parameters, agronomic characters and ion contents of the cell sap as well as dry matter to variable extent. These are discussed separately in the following paragraphs.

Gas Exchange Parameters:

High salinity decreased Pn in both the varieties (Table - 7.1). The decrease in the salt-tolerant variety LU26S was 23% while 36% decrease was noted in salt sensitive variety Punjab-85. Effect of high pH was not consistent. Generally, neither salinity nor pH affected g_s, E and Tl. However, Ci was significantly increased at high salinity and high pH. This indicates that the decrease in Pn was less due to reduced g_s and seemed to be non-stomatal in origin (Bethke and Drew, 1992). The inhibition in Pn seemed to be due to the presence of some internal resistance in the plants grown at high NaCl concentration. The sodic soils which have exchangeable sodium percentage (ESP) greater than 15, normally have an alkaline pH which is more than 8.5 (Richards, 1969). Khan (1996) reported a non-significant decrease in Pn in plants grown in soils with high ESP.

Leidi *et al.* (1991b) found that in NH_4 fed plants, E increased with an increase in pH of the nutrient solution and decreased with NaCl concentration. This effect of high pH was not visible in this study.

Leidi *et al.* (1991b) reported a decrease in chlorophyll concentration in the leaves of wheat with increase in pH of the culture medium containing NaCl. Decrease in chlorophyll contents of the leaves (Salama *et al.* 1994) might have been responsible for a slight and non-significant decrease in Pn at high pH in this study. In the experiment reported in Chapter 6, however a significant decrease in Pn was noted at pH 8.5.

Decrease in Pn due to NaCl salinity was lesser in magnitude as compared to that reported in Chapter 6 in SARC-1. The effect of high pH was also not observed in this study. This could have been due to a lower pH level used in this case (pH 8.0) as against 8.5 in the previous experiment. Another reason could be the differences in the duration of stress at the date of Pn measurements, which was about three weeks in this study as against four weeks in the previous experiment.

The effect of salinity on Pn was significantly greater in Punjab-85 than LU26S which could be a reason for its better salt tolerance.

Growth Analysis:

Leaf area and number of tillers were decreased significantly by 100 mol m^{-3} salinity in both the varieties while high pH had no significant effect (Table - 7.4). The percentage decrease in leaf area and number of tillers due to high salinity was comparatively greater in Punjab-85 than in LU26S. There was a similar decrease in fresh and dry weight per plant at 100 mol m^{-3} salinity while there was no effect of high pH. Dry weight of root was decreased due to high salinity and high pH and the decrease was greater in the salt-sensitive variety Punjab-85. Devitt *et al.* (1984) reported a decrease in wheat root weight in response to an increase in osmotic potential of the nutrient solution. Tang and Robson (1993) reported a reduction in the growth of roots and shoots in *Lupinus* species with increasing pH of hydroponic culture medium above 6.0, which resulted in decreased uptake of Fe^{2+} and phosphorus. A substantial decrease in growth of rice tops and roots at pH 8.5 was also reported by Alam (1981).

Specific leaf area was decreased by salinity but not by high pH (Table 7.6). Ratio of fresh weight/dry weight and shoot/root were significantly decreased by salinity stress (Table -7.7). Effect of pH was noted on shoot/root ratio only. It could be judged that basically small specific leaf area and secondly lower Na^+ contents of the leaf blades was related to the salt tolerance of wheat. In comparison to effects of salinity and high pH on Pn, variety x salinity interaction was significant for most of the growth analysis data and the injurious effect of salinity was greater in salt-sensitive variety Punjab-85. Comparatively high Na^+ and Cl^- contents and lower K^+/Na^+ ratio at high salinity levels, seem to be responsible for decreased leaf area, number of tillers and in some other growth parameters in the salt-sensitive variety Punjab-85 than LU26S. Super imposed high pH caused a negative influence on Na^+ and Cl^- which was more evident in Punjab-85. Decrease in K^+ was greater in LU26S than in Punjab-86.

As reported by other workers (Wyn Jones and Gorham, 1989; Läuchli and Epstein, 1990; Shalhevet *et al.* 1995), salinity reduced growth of the wheat plants through its effect on the shoot and root growth, decrease in leaf area, number and length of tillers and dry matter accumulation. The effects of salinity are influenced by changes in the plant's water status particularly that of the leaf. An increase in root zone salinity would intensify this effect by lowering the overall plant water status. It has also been reported that water deficit in the expanding tissues was responsible for decreased plant growth (Delane *et al.* 1982; Munns *et al.* 1982). With increase in age and build up of the salt concentration, other symptoms of salt injury may appear. The specific effects of salinity on leaf and other growth parameters under saline conditions could be due to excessive transport of Na^+ and Cl^- and decreased uptake of K^+, Ca^{2+}, Mg^{2+}, NO_3^- or SO_4^{2-} ions. Termaat and Munns (1986) also reported similar results. However, the lesser effect of salinity on cell sap K^+ in Punjab-85 and greater effect on growth, do not agree with the above findings. The adverse effects of salinity may be further aggravated at high pH of the growth medium (Srivastava, 1988; Leidi *et al.* 1991a, b). In this study however, the injurious effect of high salinity in combination with high pH was not observed on the majority of the yield determining components.

Ion Composition of Cell Sap:

High pH had little effect on Na^+ and Cl^- contents of the cell sap in either of the varieties but 100 mol m^{-3} NaCl salinity caused a very high increase (Table - 7.9). Na^+ and Cl^- contents of the salt-sensitive variety Punjab-85 were significantly greater than the salt-tolerant variety LU26S. Enhanced Na^+ accumulation was noted under the combined effect of high salinity and high pH. Wheat cultivars resistant to salinity and/or sodicity of soil were reported to maintain a lower concentration of Na^+ and higher concentration of K^+ and K^+/Na^+ ratio than the sensitive cultivars (Sharma, 1991). An increase in the uptake of Cl^- at high pH level of the nutrient solution has been reported by many workers (e.g. Findenegg *et al.* 1989). Padole (1991) reported a reduction in uptake of N, P, K^+, Ca^{2+}, Mg^{2+}, Zn^{2+}, Mn^{2+}, Cu^{2+} and Fe^{2+} by salinity and/or sodicity in wheat.

About 42% and 30% decrease in K^+ contents was recorded in LU26S at pH 6.0 and pH 8.0 respectively. At both the salinity levels, an increase in K^+ was noted at high pH in LU26S. This effect was also visible in Punjab-85 at pH 6.0. Higher K^+ contents at high pH, might be due to high K^+ contents of the nutrient solution at high pH due to the addition of KOH used to raise the pH of the nutrient solution. In Punjab-85, there was no effect of 100 mol m^{-3} NaCl on K^+ contents at pH 6.0 but about 15% decrease was noted at pH 8.0. The salt-sensitive variety was unable to maintain its K^+ level. This is opposite to the results reported in Chapter 6 (section 6.3.3) where K^+ contents were lower at high pH at both the levels of NaCl salinity. The trend in Punjab-85 was similar to that in LU26S at low salinity (S_0) and pH_6 but at high salinity and high pH, K^+ contents decreased significantly in Punjab-85 but not in LU26S.

Reduced K^+ uptake has been often reported in wheat plants growing in solution culture containing NaCl (Munns and Termaat, 1986; Iqbal, 1992; Watanabe *et al.* 1992; Gorham, 1994). Similar results of high NaCl concentration and high pH on K^+ uptake were also reported by Leidi *et al.* (1991a) in wheat and Alam (1981) in rice.

K^+/Na^+ ratio was decreased by NaCl salinity in both the varieties but high pH did not affect it significantly (Table - 7.11). Decrease in K^+/Na^+ ratio in the leaf cell sap of wheat genotypes grown in culture medium containing NaCl was reported also by Khan (1996). Salt-tolerant variety LU26S had higher K^+/Na^+ ratio than the salt-sensitive variety Punjab-85 in the absence of NaCl salinity while the differences were negligible at 100 mol m^{-3} NaCl salinity. Higher K^+/Na^+ ratio in the salt-tolerant variety than the salt-sensitive variety was also reported by Sharma (1991). Better tolerance to 100 mol m^{-3} NaCl salinity in leaves of LU26S, may be a result of better compartmentation of Na^+, Cl^- and K^+ between different tissues or between different compartments within cells (Gorham *et al.* 1990).

The increase in the Na^+/Ca^{2+} ratio in the solution by added NaCl may have increased the permeability of the root membranes to Na^+ and Cl^- due to a loss in root selectivity (Greenway and Munns, 1980) which might have raised these ions in the cell sap. An increase in Na^+ and Cl^- contents at high NaCl concentration and high pH of the nutrient solution was also reported by Leidi *et al.* (1991a). Yasin (1991) reported an increase in leaf Na^+ and a decrease in K^+ contents with increasing Na^+ and ESP of the soil. Sharma (1991) compared different wheat varieties at different ESP levels and found that plant Na^+ concentration was greater in the sensitive variety HD4502 than in the tolerant variety Kharchia-65. At pH 9.4 and 9.6, Na^+ concentration in the leaves of salt-sensitive variety HD4502 was greater than 2% while in Kharchia-65, all leaves had less than 2% Na^+.

Ca^{2+} and Mg^{2+} were greatly decreased in both the varieties at high salinity which caused a decrease of about 77% and 69% in LU26S at low and high pH respectively (Table - 7.10). In Punjab-85 corresponding decreases were 78% and 77% respectively. Thus the percentage decreases in Ca^{2+} were almost similar in both the varieties. Decreases in Mg^{2+} due to salinity in LU26S were about 44% at both the pH levels while the corresponding decreases in Punjab-85 were 58% and 53% at low and high pH respectively. There was a tendency for maintaining higher levels of Ca^{2+} and Mg^{2+} in LU26S than the salt-sensitive variety Punjab-85 at both stress levels.

In the pooled data for cell sap ions, there were significant negative correlations between Na^+ and Ca^{2+} (r = -0.914), Na^+ and Mg^{2+} (r = -0.728), Ca^{2+} and Cl^- (r = -0.908), Na^+ and K^{2+} (r = - 0.583) and significant positive correlation between Na^+ and Cl^- (r = 0.983). All these correlations were significant at 1% level of significance. However this data must be treated with caution as it includes only two salinity levels. Further experiments testing salinity levels over the range 0 - 200 mol m^{-3} NaCl are required to substantiate these findings. Within each salinity levels, the r values were low and non-significant.

It has been reported that Na^+ displaces Ca^{2+} at root membranes (Cramer *et al.* 1985) which might be a cause for decreased Ca^{2+} in the leaf cell sap of the NaCl treated plants. The trend for Ca^{2+} contents in this study at high pH in the absence of NaCl salinity are in agreement to those of Leidi *et al.* (1991a) who reported that concentration of Ca^{2+} in the shoots of wheat decreased with increasing pH of the growth medium containing nitrate as a source of nitrogen. Contradictory results were reported by Alam (1991) who reported an increase in Ca^{2+} and Mg^{2+} uptake with increasing pH in tops and roots of rice plants.

Ion Contents in Dry Plant Material:

Generally, the trends in Na^+ and K^+ contents in the dry matter were nearly the same as found in cell sap. Trend for K^+ contents were nearly the same in LU26S, but quite different in Punjab-85 (Table-7.12) in which decreases caused by salinity were greater than those found in cell sap. This could be due to a different pattern of K^+ accumulation in different plant parts in this variety. Ca^{2+} and Mg^{2+} contents were reduced by NaCl salinity in both the varieties. High pH also significantly decreased Ca^{2+} contents in both the varieties, while in cell sap, Mg^{2+} contents increased at high pH in LU26S, but decreased in Punjab-85 at 0 mol m^{-3} NaCl. Cl^- contents significantly increased by NaCl salinity in both the varieties but there was little effect of high pH.

High salinity caused a significant decrease in Zn^{2+}, Fe^{2+} and Mn^{2+} contents. Zn^{2+} contents were significantly decreased at high pH in both the varieties (Tables 7.15 & 7.16). At pH 6.0, salinity caused a 14% and 21 % decrease in Zn^{2+} in LU26S and Punjab-85 respectively while corresponding decreases at pH 8.0 were 27% and 7% respectively. Fe^{2+} decreased in LU26S at high salinity and high pH and the percentage decreases at pH 6.0 and pH 8.0 due to salinity were 19% and 23% respectively. In Punjab-85, the trend was not consistent. Salinity x pH interaction was significant. At low salinity, pH 8.0 caused a decrease in Mn^{2+} while at high salinity the trend was reversed. At pH 6.0, salinity caused a 39% and 49 % decrease in Mn^{2+} in LU26S and Punjab-85 respectively while corresponding decreases at pH 8.0 were 18% and 30% respectively. Hence percentage decrease was greater in the salt-sensitive variety Punjab-85 and were greater at low pH in both the varieties. Soil pH has been reported to be an important factor influencing the growth of most field crops and pastures (Christenson *et al.* 1971). The effect of soil pH is associated with changes in the solubility and availability of plant nutrients.

In spite of the fact that Zn^{2+}, Mn^{2+} and Fe^{2+} were above the adequate limits reported by Salisbury and Ross (1991), even then the pale green colour of the leaves of plants growing at pH

8.0 gave an indication of some Fe^{2+} deficiency as has also been reported by Padole (1991) and Srivastava and Srivastava (1993). The pale green colour of the leaves could also be due to possible nitrogen deficiency caused by high pH of the growing medium as proposed by Tang and Robson (1993).

Final Yield Data:

Salinity resulted in a significant decrease in grain weight per plant in both the varieties but the decrease was larger in the salt-sensitive variety Punjab-85 than the salt-tolerant variety LU26S (Table - 7.21). In the absence of NaCl salinity, grain weight per plant was greater in Punjab-85 while at 100 mol m^{-3}, LU26S gave larger grain weight. There was no effect of pH on grain weight. Salinity x pH and variety x pH interactions were non-significant i.e. the effects of salinity and pH were the same for salt-tolerant and salt-sensitive varieties. Salinity decreased the grain yield in both the varieties due to its effects on ears, number of grains and size of grains. Smaller and fewer ears, fewer grains per ear and smaller grains at 100 mol m^{-3} than at 0 mol m^{-3} NaCl were responsible for decreased yield. LU26S had fewer grains per plant due to fewer fertile spikelets per ear as compared to Punjab-85 (Table - 7.18), but had larger grains as shown by greater 100 grain weight (Table - 7.22). In spite of lower number of grains in LU26S at high salinity (Table - 7.21), its grain weight per plant was higher than Punjab-85 possibly due to salinity induced enhanced translocation of assimilates from the flag leaves to developing grains (Leidi and Lips, 1990). Decrease in the number of grains in wheat genotypes at high NaCl salinity was also reported by Khan (1996). In a pot experiment, Padole (1991) irrigated wheat with highly saline sodic waters and noted a significant decrease in yield. It was also reported that combined effect of salinity and sodicity were greater than salinity alone. Grain and straw yields were also decreased at an ESP of 38.5 (3.6 dS m^{-1} salinity) and an ESP of 56.4 (4.45 dS m^{-1} salinity).

Harvest index was significantly decreased at 100 mol m^{-3} NaCl salinity and the effect was more in the salt-sensitive variety Punjab-85 (Table - 7.22). Harmful effect of 100 mol m^{-3} salinity in combination with high pH was significantly more injurious in Punjab-85. Effect of high pH was not visible in the salt-tolerant variety LU26S. Khan (1996) found a greater harvest index in salt-tolerant genotype of wheat and reported a significant decrease at high ESP of soil.

7.5 CONCLUSIONS

NaCl salinity caused a decrease in Pn but there was little effect of high pH in the absence of NaCl stress. Pn was greater in LU26S which might be a reason for its better salt tolerance. During the vegetative phase, salinity at 100 mol m^{-3} NaCl caused a significant decrease in most of the growth parameters while there was no effect of high pH.

At maturity, high salinity reduced all the growth and yield parameters. High pH had little effect on other parameters and yield components. At high salinity, LU26S was able to maintain a higher leaf area per plant during vegetative phase, total green leaf area at 60 DAS, total fresh and dry weight/plant which could be a reason for its better salt tolerance.

High salinity caused an increase in Na^+ and Cl^-, and a decrease in K^+, Ca^{2+}, Mg^{2+}, K^+/Na^+ ratio, Zn^{2+}, Fe^{2+} and Mn^{2+}. High pH induced an increase in Na^+, K^+, Cl^-, K^+/Na^+ and a decrease in Zn^{2+}, Fe^{2+} and Mn^{2+}. LU26S was found high in Ca^{2+}, Mg^{2+}, K^+/Na^+ ratio in cell sap as well as dry matter; and Zn^{2+}, Mn^{2+}. Lower K^+/Na^+ and high accumulation of Na^+ and Cl^- in Punjab-85 could be the reason for its salt sensitivity which caused greater sterility and reduced its per plant yield. Generally, weight of grains per plant and 100 grain weight was greater in LU26S. Better grain yield of LU26S at 100 mol m^{-3} NaCl salinity was due to higher 100 grain weight and not due to higher number of grains per plant.

CHAPTER 8

GENERAL DISCUSSION

CHAPTER 8

GENERAL DISCUSSION

It is difficult to conduct replicated field experiments in salt affected soils under standardized conditions due to soil heterogeneity. Hence most of the research work is being conducted using hydroponic culture methods in glass house or growth rooms. NaCl alone or a mixture of salts are generally used for creating salt stress in these studies. Considerably less research has been conducted on the combined problems of salinity and sodicity in the field as well as green house. Hence the research reported in this thesis, broadly addressed these two areas i.e.

1. Comparison of responses of wheat to saline and sodic soil conditions.
2. Comparison of growth and performance of wheat under field conditions (saline and sodic soil) and solution culture conditions (acidic and alkaline pH).

Experiments at Pindi Bhattian (saline soil conditions) and Sadhuke (sodic soil conditions) in Pakistan and glasshouse and growth room experiments in the University of Wales, Bangor, UK did not include all the same varieties. All the wheat varieties sown in the sodic soil (section 4.2.1.1, pages 54-55) could not be sown under the saline conditions (section 3.2.1.1, page 35) due to problems regarding seed availability. Similarly all the varieties included in Experiment 1 (section 2.2.1, page 12) could not be included in other experiments in solution culture (Chapter 5, 6 and 7) due to other limitations. The wheat varieties included in different experiments along with their respective growth media are presented in Table - 8.1.

Experiment 1 (Chapter 2) showed that different growth parameters and yield components decreased with an increase in salt stress. Decreases in these parameters by salt stress have been reported by other research workers (Dale, 1982; Munns and Termaat, 1986; Neumann *et al.* 1988; Ashraf and McNeilly, 1991; Pessarakli *et al.* 1991; Kalaji and Nalborczyk, 1991; Mahmood and Quarrie, 1993; Francois *et al.* 1994). Decreases in leaf area and dry weight were consistently associated with a decrease in grain weight as is evident from values of linear correlation for pooled data of all varieties (Table - 2.11). Decrease in weight of grains per spike by salinity was also related with a decrease in RGR. SARC-1 variety having highest RGR at 150 mol m^{-3} NaCl

Table 8.1: List of wheat varieties included in different experiments reported in the thesis and the respective medium of growth

No. of experiments →	1	2	3	4	5	6
No. of chapters →	2	3	4	5	6	7
Growth medium →	Solution culture (UK)	Saline soil Pakistan	Sodic soil Pakistan	Solution culture (UK)	Solution culture (UK)	Solution culture (UK)
SARC-1	✓	✓	✓	-	✓	-
SARC-2	-	✓	✓	-	-	-
SARC-3	-	✓	✓	-	-	-
SARC-4	-	✓	✓	-	-	-
LU26S	-	✓	✓	✓	-	✓
Punjab-85	✓	✓	✓	✓	-	✓
Pato	-	-	✓	-	-	-
7-Cerros	-	-	✓	-	-	-
PAK-81	✓	-	✓	-	-	-
Kharchia-65	✓	-	✓	-	-	-

Note : The varieties having a tick (✓) were included in the respective experiments while those with a (-) sign were not included.

gave the highest grain weight per spike and Punjab-85 had the lowest grain weight which was associated with the lowest RGR (Table 2.9, page 26). Comparatively better yield and salt tolerance of Kharchia-65 and SARC-1 seemed to be due to their ability to maintain higher leaf area and dry weight under salt stress. Punjab-85 seemed to be an excellent variety for non-saline conditions. The causes of its salt sensitivity appeared to be due to harmful effects of salts on leaf area (Table 2.1, pages 17-18), dry weight (Table 2.2, page 20) and RGR (Table 2.9, page 26). Salt tolerance of Kharchia-65 has been attributed to maintenance of higher leaf area under saline or alkaline conditions (Srivastava *et al.* 1988; Gupta and Srivastava, 1989). In this study, high grain weight per spike (Table 2.10, page 27) was not consistently associated with either greater number of grains per spike or heavier grains. Deleterious effects of NaCl stress could be due to an excessive accumulation of toxic ions i.e. Na^+ and Cl^- in cell sap or the plant tissues (Gorham *et al.* 1990; Omielan *et al.* 1991) or due to decrease in water potential (Richards, 1969). Availability of water to plants is a big problem in saline soil conditions. Plants are not able to use a large portion of soil moisture in the saline soil that is normally available under non-saline soil conditions. This implies that the responses to salt stress might be different in solution culture studies as compared to saline field conditions (Richards, 1992). Hence experiments were planned in Pakistan under actual saline and sodic field conditions to compare the results obtained under greenhouse conditions and to study the uptake of toxic ions by different wheat varieties.

Comparison between saline soil and solution culture conditions:

Experiment 2 (Chapter 3) on a saline soil characterized by a medium to high salinity during the growth period had soluble salts ranging from 97 mol m^{-3} (9.7 dS m^{-1}) to 127 mol m^{-3} (12.7 dS m^{-1}), according to the conversion proposed by Richards (1969), which almost corresponded to 100 mol m^{-3} and 150 mol m^{-3} in the solution culture experiments (Chapters 2, 5, 6 & 7). The dominant salt was NaCl. Highest grain weight per spike was found in the salt-tolerant variety LU26S and the lowest in the salt-sensitive variety Punjab-85. There were non-significant differences in leaf area between the varieties at both the sites (normal and saline) hence contribution of leaf area towards better performance of LU26S or poor performance of Punjab-85 is not clear. There was however a very close relationship of Na^+ contents and K^+/Na^+ ratios in flag leaves with the grain yield in LU26S. This salt-tolerant variety had the lowest Na^+ contents and the highest K^+/Na^+ ratio as opposed to the salt-sensitive variety which had the highest Na^+

contents and lowest K^+/Na^+ ratio. However, when the data for all varieties were included, the correlations were non-significant. Maintenance of low internal Na^+ and high K^+ and K^+/Na^+ ratio has been quoted as a mechanism of salt tolerance in wheat by different authors (Shannon, 1978; Sharma, 1991; Qadar, 1993). There was a close relationship of dry weight of main shoots with the grain weight per spike.

There was a close relationship of total leaf area with the grain weight in the solution culture and saline soil experiments. However, in Experiment 1, total leaf area per plant was recorded (Table - 2.1, page 17) while in saline soil, only flag leaf area was recorded (Table - 3.2, page 42). Percentage decreases in different yield parameters were calculated for two wheat varieties (SARC-1 and Punjab-85) grown under the two systems i.e. saline solution culture and saline soil (Table - 8.2, page 187). The effects of salinity under saline soil conditions were less severe than under greenhouse conditions for most of the growth parameters especially in SARC-1 e.g. leaf area, number of tillers, weight of grains per ear and 100 grain weight. However, all the parameters were not affected in the same way and the responses of salt-sensitive variety Punjab-85 were different from those observed for salt-tolerant variety SARC-1. This might be due to fluctuating salinity as a result of irrigations with good quality water in this light textured soil, and some rainfall, and hence subsequent leaching of excessive salts beyond the root zone. Fluctuating salinity has been reported to be less injurious to wheat as compared to the continuous salinity under solution culture (Iqbal, 1992; Francois *et al.* 1994). It is difficult to compare soil and solution culture by this methodology because the soil had large amounts of Ca^{2+}, while in the solution culture experiment no additional Ca^{2+} was added except that present in Phostrogen. Ca^{2+} is known to decrease the damaging effect of Na^+ in plants (Ehret *et al.* 1990). There were also major environmental differences between the saline site in Pakistan and the greenhouse in Bangor, UK which might be responsible for this differential response. However, in this respect one might have expected comparatively greater effects of salinity in Pakistan, as a result of hotter, drier conditions favouring rapid transpiration and greater salt uptake. Ahsan (1996) also recorded lower grain weight per plant in wheat under saline solution culture conditions than under saline soil conditions and attributed this to increase in temperature of the greenhouse during grain filling stage.

At 150 mol m^{-3} salinity in solution culture, decrease in grain weight per spike (Table 2.10, page 27) ranged between 40% and 65% in different varieties while in saline soil (97 to 127 mol

m^{-3} salinity stress), the decrease in grain weight per main spike ranged between 13% and 52% (Table 3.8, page 47). Due to problems of seed availability, Kharchia-65 and PAK-81 which were sown in solution culture (Experiment 1), could not be sown in saline soil in Pakistan. Hence LU26S (local salt-tolerant variety) along with some other varieties were sown in the saline soil. The decrease in grain weight in the most salt tolerant variety Kharchia-65 in solution culture was 65% while in saline soil the salt-tolerant variety LU26S suffered 14% decrease in grain weight. The decreases in grain weight in SARC-1 and Punjab-85 in saline solution culture were 40% and 57% respectively while in saline soil the corresponding decreases were 22% and 47% respectively. This differential response in these two varieties shows that decreases in grain weight in both the experiments were less severe in the saline soil but the percentage decreases followed the same trend in both of these studies. This suggests that the results obtained in solution culture experiments might be helpful for predicting their behaviour in saline field conditions but the relative performance may be different due to environmental conditions. Although absolute grain weight of salt-tolerant variety Kharchia-65 was greater than PAK-81 and Punjab-85, the percentage decreases in grain weight per spike, number of grains per spike and 100 grain weight were greater in this variety than in all the other varieties.

In the solution culture experiment, 150 mol m^{-3} NaCl caused decreases in dry weight of main shoots in SARC-1 and Punjab-85 of 65% and 68% (at 60 DAS) respectively. Decreases in grain weight (Table - 8.2) were comparatively less severe (40% and 57% respectively). In saline soil also, effects of salt stress on SARC-1 and Punjab-85 were more severe on dry weight of shoots (35% and 55% respectively) than its effects on grain weight (22% and 47% respectively). This suggests that the effects of salinity on vegetative growth were greater than effects on reproductive growth.

In saline solution culture and saline soil, SARC-1 gave better grain weight than Punjab-85. At 150 mol m^{-3} NaCl stress in solution culture, SARC-1 gave 35% more grain weight than Punjab-85 while in the saline soil the corresponding increase in SARC-1 was 32%.

High K^+/Na^+ ratios are usually associated with better salt tolerance in wheat (Kemal-ur-Rahim, 1988; Omielan *et al.* 1991; Sharma, 1991; Iqbal, 1992; Maliwal and Sutaria, 1992; Ahsan, 1996; Khan, 1996). In Experiment 1, K^+ and Na^+ were not measured but in other experiments conducted in solution culture (Experiments 4 and 6), high K^+/Na^+ ratios were not associated with better salt tolerance except in older leaves in Experiment 4. This might be due to the fact

Table - 8.2: Percentage decreases relative to control in different growth parameters by salinity stress in solution culture (Experiment 1, Chapter 2), and saline soil (Experiment 2, Chapter 3)

Parameters	Solution culture		Saline soil	
	SARC-1	Punjab-85	SARC-1	Punjab-85
Leaf area	74	68	54	50
Weight of main shoots	65	68	35	55
Weight of ears	39	34	25	46
Number of tillers/plant	50	39	40	49
Number of ears/plant	46	50	43	58
Weight of grains/ear	40	57	22	47
100 grain weight	23	40	1	11

Note-1: In solution culture, decreases were calculated at 150 mol m^{-3} NaCl over control (0 mol m^{-3} NaCl) at 60 DAS.

Note-2: In saline solution culture, total leaf area/plant at 60 was used for these calculations, while in saline soil, flag leaf area was used.

that in solution culture experiments (4 & 6), salt stress levels were lower than in the saline soil in the field. Another possible reason could be the duration of exposure to salinity which was considerably greater in saline soil than in saline solution culture.

Comparison between sodic field conditions with alkaline solution culture conditions:

The sodic soil was characterized by a low salinity and high pH and high ESP. The soil was dispersed due to high ESP. Porosity and hydraulic conductivity were not measured but were likely to be very low. The concentration of soluble salts at the sodic site was about 31 to 40 mol m^{-3} during the tenure of the experiment, the dominant salt being NaCl. ESP of the soil was higher than 15, pH was more than 8.5 and it was classed as 'sodic' (Richards, 1969).

Although it is difficult and perhaps rather inappropriate to make comparisons for different parameters in between these two systems, due to differences in EC_e and pH, apart from differences in growing medium, the effects of the growing conditions on percentage decreases or increases for different parameters are presented in Table - 8.3 (page 189). These comparisons have been made only for two varieties i.e. LU26S (salt-tolerant) and Punjab-85 (salt-sensitive). There were very large decreases in different parameters in the sodic soil; accompanied with a large increase in Na^+ contents which was comparatively greater in Punjab-85. Compared with the 'S_0pH_8' in solution culture (e.g. Tables 7.1, page 142 & 7.4, page 146), the deleterious effects of salt stress were very severe in the sodic soil. However, the effects were more severe in solution culture at '$S_{100}pH_8$'. Severe effects under sodic soil conditions might be due to poor growing conditions caused by poor soil structure, owing to high ESP (Richards, 1969). Although wheat has been classified as tolerant to ESP of the sodic soil in the range of 40 - 60 (Bresler *et al.* 1982), large decreases in different growth parameters were noted in this experiment (e.g. Tables 4.2, page 62 & 4.3, page 63) at about 20 ESP due to very poor physical conditions of the soil. Greater decreases in different parameters at 'S_{100} pH_8' were possibly due to combined effect of high salinity and alkaline conditions (Padole, 1991; Sharma, 1991). The adverse effect of high ESP on the yield and other parameters have also been reported by different workers (Singh *et al.* 1990; Yasin, 1991; Khan, 1996).

Apart from high ESP, there was about 31 to 112% more soluble Na^+ in sodic soil than the normal site while the associated decreases in grain weight were 34% and 37% in LU26S and Punjab-85 respectively. The flag leaves of LU26S had considerably lower Na^+ content (about

Table - 8.3: Comparison of percentage increases (+) or decreases (-) in different parameters due to sodicity (high pH) at sodic soil in field and alkaline solution culture in the glasshouse.

Parameters	Sodic soil		Alkaline solution culture			
	LU26S	Punjab-85	LU26S		Punjab-86	
			S_0 pH_8	S_{100} pH_8	S_0 pH_8	S_{100} pH_8
Leaf area	- 52	- 60	- 2	- 54	+ 3	- 67
Pn	- 6	*	- 5	- 28	- 9	- 27
Main shoot weight	- 52	- 54	+ 20	- 68	- 7	- 85
Total tiller number	- 44	- 36	- 9	- 22	+ 21	- 36
Total spike number	- 50	- 44	+ 22	- 47	- 1	- 64
Na^+ dry matter	+ 4650	+ 5549	+ 5	+ 1300	+ 5	+ 1216
K^+ dry matter	- 21	- 24	+ 2	- 29	+ 4	- 28
K^+/Na^+ dry matter	- 98	- 99	- 4	- 95	+ 1	- 95
Number of grains	- 18	- 23	+ 26	- 71	+ 7	- 84
Weight of grains	- 34	- 37	+ 17	- 76	- 8	- 93
100 grain weight	- 23	- 22	- 6	- 21	- 2	- 53

Note 1: In sodic soil, flag leaf area while in solution culture total leaf area was used for calculating percentages.

Note 2: Na^+, K^+ and K^+/Na^+ ratio are from dry flag leaves from experiment in sodic soil; and dry matter at 38 DAS from experiment in alkaline solution culture.

Note 3: In the experiment conducted in solution culture, percentage decreases or increases were calculated in treatment 'S_{100} pH_8' as compared to the treatment ' S_0 pH_6'.

* : Data not recorded.

27%) than Punjab-85 and gave about 10% more grain weight per spike which indicates its better tolerance to sodicity than Punjab-85. Decrease in K^+/Na^+ ratio in flag leaves of both LU26S and Punjab-85 was about 98% as compared to the normal soil, but LU26S gave about 10% more grain weight than Punjab-85 as reported above.

In Experiment 6, the increases in Na^+ and decrease in K^+ contents (in both cell sap and dry matter) were associated with decrease in grain weight in both the varieties. About 8500% increase in Na^+ was noted in 'S_{100} pH_8' treatment in cell sap (1300% in dry matter) as compared to 'S_0pH_6' in LU26S which caused about 76% decrease in grain weight. The corresponding decrease in salt-sensitive variety Punjab-85 was about 93% which was caused by about 9000% increase in Na^+ in cell sap as compared to 'S_0pH_6'. Greater decrease in grain weight in this experiment than sodic soil was due to combined effect of high salinity, high pH and high Na^+ contents in the plants.

Comparison between saline and sodic field conditions:

The saline soil was characterized by the presence of high concentrations of soluble salts (Table 3.1, page 38). The EC_e of the saline soil was 12.7 dS m^{-1} at the time of sowing and 15.8 dS m^{-1} at the time of harvest. It was comparatively lower at booting. ESP and pH were less than 15 and 8.5 respectively. The soil was sandy loam, flocculated with no permeability problem. The sodic soil on the other hand had an EC_e ranging from 3.1 - 4.0 dS m^{-1} while the ESP and pH ranged from 19.1 - 22.2 and 8.7 - 9.7 respectively (Table - 4.1, page 56). Due to high amounts of exchangeable Na^+ these soils are dispersed and lose their flocculation, with little permeability to water and air (Richards, 1969). The plants responded differently to these different physical and chemical characteristics of the soil. The main differences observed in wheat plants on these two types of soils are as follows:

K^+/Na^+ ratio was lower under sodic conditions than under saline soil conditions. The leaves had greater Na^+ and lower K^+ contents under sodic soil conditions than under saline soil conditions. Increasing ESP of the soil results in decreased accumulation of Ca^{2+}, Mg^{2+}, and K^+ in plants (Richards, 1969). Contribution of flag leaves to daily production rates is about 50-60% (de Vos, 1979; Thorne, 1982) and a large variation of about 25% in Pn rates in flag leaves of different wheat varieties has been reported by different researchers (e.g. Dantuma, 1973). In Punjab-85, flag leaf area was decreased more in sodic soil (60%) than in saline soil (50%), while the difference was not so significant in LU26S. Total number of tillers and spikes decreased more in sodic than saline soil. Excessive Na^+ in the soil might have exerted important secondary effects on plant growth through adverse structural modifications of the soil (Richards, 1969). Punjab-85 had heavier spikes and greater grain weight in the sodic soil than in the saline soil. In LU26S, the trend was reverse of Punjab-85. This shows that the better tolerance of Punjab-85 to sodicity rather than salinity was mainly due to maintaining higher number of grains per spike. Number of tillers were also significantly lower in the sodic soil as compared to the saline soil, possibly due to the dense nature of the soil which might have inhibited tillering. Singh and Rana (1985) studied genetic variability in different wheat varieties on a sodic soil using specially designed concrete blocks and reported that grain yield was positively and significantly correlated with K^+ contents in the leaves while there was a significantly negative association with the Na^+ contents. They further argued that Na^+ and K^+ contents in the leaves at the tillering growth phase may be used as a reliable criteria for predicting the grain yield of wheat grown in sodic soils.

The varieties which performed better under saline soil conditions did not necessarily do so under sodic soil conditions. In saline soil, LU26S, SARC-2 and SARC-4 gave higher grain weight than the other varieties while SARC-3 and Punjab-85 gave the lowest grain weight (Table 3.8, page 47). In contrast to this, LU26S, SARC-4 and Punjab-85 gave the highest grain weight per spike in sodic soil while SARC-1 gave the lowest grain weight and proved sensitive to sodicity (Table 4.11, page 73). From this, it can be concluded that the varieties bred and selected for saline environments will not necessarily do well in predominantly sodic environments and vice versa.

Comparison between high and low pH in solution culture:

pH of the nutrient solution altered the effects of salinity especially in Experiment 5 (Chapter 6). The results from Experiment 5 (Chapter 6) furnish some indication that the effects of 100 mol m^{-3} NaCl salinity on gas exchange, growth and uptake of toxic ions were greater at high pH (pH 8.5) than at low pH (pH 5.8). Percentage decreases in root and shoot weight, leaf area due to salinity were greater at high pH than at low pH. Increases in concentrations of toxic ions were also greater at high pH than at low pH. The harmful effects of high pH in combination with high salinity might be due to effects on gas exchange or due to decrease in nitrogen concentration as suggested by Tang and Robson (1993). A salt-tolerant variety SARC-1 was used in this experiment. These results need to be verified on the basis of further research.

Generally the combined effect of high salinity and high pH was more harmful and severe than high salinity or high pH alone in Experiment 5. These adverse effects were conspicuous on different gas exchange parameters (Pn, g_s and E), growth parameters (number of tillers, leaf area, dry weight), ion uptake (Na^+, K^+ and Cl^-). These effects were comparatively less severe and non-significant on gas exchange parameters, number of tillers per plant, total leaf area and dry weight per plant at pH 8.0 in Experiment 6 (Chapter 7). The reasons for these differences in response between Experiments 5 and 6, are unclear, and are discussed in the next section. The contents of Na^+ and Cl^- in the leaves were significantly increased while Zn^{2+} and Mn^{2+} were decreased. There was no significant decrease in Fe^{2+} uptake at high pH (Table 7.15, page 163) which is contrary to the results obtained by Leidi *et al.* (1991a), and interveinal chlorosis noted in the wheat plants in Experiment 6.

The results of the field experiments on saline and sodic soils indicated that plants took up more Na^+ and comparatively less K^+ in the sodic soil (pH > 8.5) than those in the saline soil (pH < 8.5). Although soil pH was in the alkaline range in both these experiments, the adverse effects were more severe in the sodic soil which had a higher pH. However, these severe effects might also be partly due to high ESP in this sodic soil having degraded soil structure (Richards, 1969; Muhammed, 1993).

On the basis of the preceding experimental results and ensuing discussion, it is evident that the varieties performing better under saline environments may not do so under sodic conditions. Hence it can be suggested that for selecting and breeding varieties for sodic soils, the testing needs preferably to be done under alkaline solution culture medium, although much care will be needed to avoid possible nutrient deficiencies.

It is also concluded that evaluation of different varieties of cereals under alkaline solution culture conditions does not give a better indication of their potential performance under saline or sodic soil conditions than evaluation under acid solution culture conditions. This may be mainly due to the fluctuating pattern of soil salinity during growth and effects associated with soil structure under sodic field conditions.

Comparison between alkaline solution culture experiments at pH 8.0 and pH 8.5 :

Comparisons of the data collected in Experiments 5 and 6 indicated the following main differences.

The injurious effects of '$S_0pH_{8.5}$' and '$S_{100}pH_{8.5}$' on Pn (Table - 6.1, page 122) were more severe than 'S_0 pH_8' and 'S_{100} pH_8' (Table - 7.1, page 142) respectively. These effects were associated with similar effects on g_s. Ci was found to be greater at '$pH_{8.5}$' than at 'pH_8' but the trends were not consistent in both the varieties, which suggest that Ci might be a limiting factor at high pH under these experimental conditions. This indicated that both stomatal and non-stomatal factors were affected at high pH and the effects were more severe at '$pH_{8.5}$' than those at 'pH_8' (Kingsbury *et al.* 1984; Rawson, 1986). Khan (1996) however did not notice any significant effect of increasing ESP (which is associated with high pH) levels on Pn in wheat.

Percentage decreases or increases in Pn and g_s due to high salinity and high pH over their respective controls (Table - 8.4, page 194) were always greater at 'S_0 $pH_{8.5}$' and/or 'S_{100} $pH_{8.5}$' than 'S_0 pH_8' and/or 'S_{100} pH_8'. It is also clear from this table that Pn decreased more in the salt-sensitive variety Punjab-85 than the salt-tolerant variety LU26S. Leidi *et al.* (1991b) noted a decrease in Pn and g_s with increase in pH of the nutrient solution. According to Devitt *et al.* (1984), the functioning of stomata may be affected adversely in leaves having low Ca^{2+} and high Na^+ concentrations even in the presence of adequate concentrations of K^+.

Combined effect of high salinity and high pH on leaf area, dry weight of roots and shoots was more severe at $pH_{8.5}$ than at $pH_{8.0}$.

K^+ uptake was decreased by about 14% in SARC-1 (Table - 6.6, page 128) by '$pH_{8.5}$' in spite of the fact that K^+ concentration in the nutrient solution was higher than at low pH as KOH was added to increase pH. This phenomenon was not evident at $pH_{8.0}$ in LU26S or Punjab-85 (Table 7.9, page 154). K^+/Na^+ ratio was lowered by about 10% at $pH_{8.5}$ (Table 6.6, page 128) due to decreased uptake of K^+ while it was increased at $pH_{8.0}$ (Table 7.11, page 157) due to an increase in K^+ uptake. Hence a small increase in pH from 8.0 to 8.5 had a large effect on K^+ contents of leaf cell sap. However, the effect in this experiment could also be due to possible higher sensitivity of SARC-1 than LU26S and Punjab-85 as can be judged from its lowest K^+ contents under sodic soil conditions (Table 4.9, page 70).

Effects of Na^+ and Cl^- on net photosynthesis :

Biomass production in plants depends on the accumulation of carbon products assimilated during photosynthesis (Terry and Waldron, 1984; Lawlor, 1987). This in turn depends on two factors i.e. the rate of photosynthesis per unit area and the surface area available for photosynthesis. The results of this study and those of other workers (Kingsbury *et al.* 1984;

Table - 8.4: Comparison of percentage decreases (-) or increases (+) in Pn and g_s at high salinity and high pH in Experiment No. 5 (Chapter 6) and Experiment No. 6 (Chapter 7)

Treatments	SARC-1		Treatments	LU26S		Punjab-85	
	Pn	g_s		Pn	g_s	Pn	g_s
$S_0pH_{5.8}$	-	-	S_0pH_6	-	-	-	-
$S_0pH_{8.5}$	- 26	-25	S_0pH_8	- 5	+ 4	- 9	- 13
$S_{100}pH_{5.8}$	- 42	- 52	$S_{100}pH_6$	- 23	- 31	- 36	- 23
$S_{100}pH_{8.5}$	- 63	- 69	$S_{100}pH_8$	- 28	- 0	- 27	- 10

Note: Percentage decreases or increases were calculated in the treatments over their respective controls i.e. '$S_0pH_{5.8}$' in SARC-1 and 'S_0pH_6' in LU26S and Punjab-85.

Rawson, 1986; Bethke and Drew, 1992; Kemal-ur-Rahim, 1988; Iqbal, 1992) show that both of these parameters are affected by salt stress. Rate of photosynthesis is usually lower in NaCl treated plants and may decrease with time of exposure to a given NaCl concentration (Munns and Termaat, 1986).

In the experiments reported in Chapters 4, 5, 6 and 7, decrease in Pn at high salt stress was always associated with high contents of Na^+ and Cl^- in the cell sap and/or dry matter. In these studies, g_s was also decreased in plants kept at high salt stress. Effect of sodicity stress in the field (Chapter 4) was most severe for decreasing Pn and g_s in wheat varieties possibly due to the effect of greater Na^+ uptake along with falling water status and consequent loss of leaf turgor (Gollan *et al.* 1986) which might have intensified the stomatal closure and thus had greater adverse effect on Pn. Low availability of water to plants is a big problem in saline soils conditions.

High Na^+ concentration in the flag leaves of different wheat varieties could also be thought a cause of decrease in Pn at the sodic site but this might not be the sole cause because PAK-81 had very low Na^+ at the sodic site but its Pn was lower than LU26S which had about 26% more Na^+. Decreases in Pn and g_s were associated with a decrease in Ci which indicated that decreased Pn was mainly due to stomatal limitations. Cl^- contents in the plants growing on saline nutrient solutions were also very high. Excessive Cl^- contents of the leaves is also reported to be a cause for decreased Pn (Rawson, 1986; Heuer and Feigin, 1993).

In Experiment 4, Pn was decreased significantly only in the young leaves in LU26S and Punjab-85 which was accompanied by a similar decrease in g_s but there was little effect on Ci which indicated that both stomatal and non-stomatal factors were influenced by excessive uptake of salts and thus affected internal and mesophyll resistance (Kingsbury *et al.* 1984; Rawson, 1986; Iqbal, 1992) whereas in Experiments 5 and 6, decreases in Pn in both the varieties due to NaCl stress and high pH also seemed to be due to both stomatal and non-stomatal factors.

High salt concentrations in the cells may damage enzymes and organelles (chloroplasts) in which photosynthesis takes place (Läuchli and Epstein, 1984). Inhibition of photosynthetic ability by excessive Cl^- has been reported by Bethke and Drew (1992). Decrease in Pn due to NaCl stress is usually caused by osmotic effects caused by excessive uptake of salts on internal and mesophyll resistance (Kingsbury *et al.* 1984; Rawson, 1986) and also due to higher contents of Na^+ and Cl^- of the leaves. This effect was more evident in the salt-sensitive variety Punjab-85 than LU26S. Omielan *et al.* (1991) reported that increase in salt tolerance in salt-tolerant wheat lines was associated with the exclusion of Na^+ and Cl^- and inclusion of K^+. They further observed that salt tolerance was correlated negatively with Na^+ and positively with the K^+ in the flag leaves and also with K^+/Na^+ ratios. The relation was suggested to be strong enough for exploitation as selection criteria in breeding for salt-tolerance in wheat.

Both rate of net photosynthesis and leaf area were reduced in SARC-1 by 100 mol m^{-3} stress as well as high pH (pH 8.5) in Experiment 5 which resulted in large reductions in total dry matter accumulation. Pn was decreased by 26%, 42% and 63% at $S_0pH_{8.5}$, $S_{100}pH_{5.8}$ and $S_{100}pH_{8.5}$ respectively as compared to $S_0pH_{5.8}$. Decreases in per plant leaf area were 62% and 74% at $S_{100}pH_{5.8}$ and $S_{100}pH_{8.5}$ respectively as compared to $S_0pH_{5.8}$. This indicated that combined effect of salinity and high pH was more severe on both Pn and leaf area. In Experiment 6, the effects of pH on both Pn and leaf area were non-significant. However, salinity did cause significant decreases in leaf area and Pn in both salt-tolerant variety LU26S and salt-susceptible variety Punjab-85. Hence the effect of these stresses on biomass accumulation and yield reduction is enhanced by the combined influence of decreased Pn rate and decreased leaf area. Krieg (1983) argued that stress reduces the efficiency of existing leaf area through reduction in rate of net photosynthesis. One of the factors identified for better salt tolerance of LU26S was its capability to maintain comparatively higher green leaf area at 60 DAS. Hence long green leaf area duration might serve as a suitable selection criteria for salinity and/or sodicity tolerance in wheat in the presence of the appropriate stress.

Effect of leaf age on net photosynthesis :

The results obtained in Experiment 4 showed that Pn increased with leaf age up to 40 DAS and then decreased (Table - 5.2, page 96). This trend was observed in both the varieties (salt-tolerant and salt-sensitive), in the absence as well as presence of 100 mol m^{-3} NaCl salinity. The differences in age had only a small effect on Pn at low PPFD values, and became more and more clear with an increase in PPFD. Osman and Milthorpe (1971) reported that rate of photosynthesis in wheat reached a maximum soon after leaf emergence and then declined and this was attributed to differences in carboxylation reactions involved in the conversion of CO_2 to carbohyderates. Later on, similar effects of leaf age on Pn were also reported by other workers (Austin *et al.* 1982; Rawson *et al.* 1983; Kemal-ur-Rahim, 1988). Dantuma (1973) reported that the effects of leaf age on rate of photosynthesis were largely due the rate of leaf senescence.

The results of Experiment Nos. 1, 2 and 3; where many varieties were used, show that different plant traits were affected differently in different varieties. It seems advisable that in such studies, use of fewer varieties with contrasting characteristics of salt tolerance (a salt-tolerant and a salt-susceptible) may be more helpful to precisely identify the traits responsible for imparting salt tolerance because in a large number of varieties, the trends become less clear and explicit.

Preceding discussion in this and other chapters suggests that variable responses of different varieties to salt tress were mainly due to the ability of the individual varieties to exclude salts from their system through selective absorption. The salt-tolerant variety LU26S was able to exclude Na^+ more effectively and generally was able to maintain greater K^+ and K^+/Na^+ ratios in its cells than the sensitive variety Punjab-85. It can be concluded also that due to spatial variability in the saline and sodic fields, quite variable responses can be expected compared to those under growth room or greenhouse conditions due to the additional deleterious effects of a degraded soil structure which may be associated with poor aeration, poor hydraulic conductivity resulting in drought like conditions and disturbed nutrition. The decrease in Pn and g_s at high salinity and/or high pH seemed to be due to both stomatal resistance and increase in internal resistance whereby chloroplasts were not able to fix CO_2 due to the presence of excessive/toxic amounts of Na^+ and Cl^- ions. Accumulation of high amounts of toxic ions as a function of time of exposure to salinity or sodicity was responsible for an early senescence and decrease in photosynthetically active surface area which was responsible for differential responses to salt-stress in these varieties of contrasting salt-tolerance. One of the characters the breeders need to look at for breeding salt-tolerant varieties should be the varietal character for maintaining sufficient green leaf area in plants exposed to external salinity during the grain filling stage. This character may also be used as a selection criterion for screening wheat varieties for salinity and sodicity tolerance. Attention of the breeders is also drawn towards the superior performance of 7-Cerros under sodicity stress, which may be exploited for wheat breeding for saline and sodic soils.

For future research, further work on the effects of alkaline pH (>pH 8.0) at high NaCl salinity, on gas exchange and growth in wheat is needed to confirm the results obtained in this study and to investigate whether these responses are due to effects on enzymes, decreased nitrogen contents at high pH, excess of toxic ions in the leaves or due to effects on nutrient availability. Further research work is also recommended to determine the reasons for failure of salt-tolerant variety Kharchia-65 to maintain high yield under sodic conditions.

LU26S which is known for its salinity tolerance can also be recommended for cultivation on sodic soils while 7-Cerros may be preferred as the best variety for cultivation on non-saline sodic soils or the sodic soils having low salinity.

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APPENDICES

APPENDICES

Appendix - A: Composition of the nutrient solutions used in solution culture experiments

Nutrients materials	Quantity (ml) of stock solution per litre
(a) Phostrogen in Experiment No. 1	1.0 gram per litre
Phostrogen in Experiment No. 4, 5 & 6	0.5 gram per litre
(b) Modified Long Ashton nutrient solution	
NaFeEDTA (37.3 g per litre stock solution)	0.5
H_3BO_3 (31.0 g per litre stock solution)	0.1
$NaMoO_4$.H2O (1.2 g per litre stock solution)	0.1
$MnSO_4.4H_2O$ (22.3 g per litre stock solution)	0.1
$CuSO_4.5H_2O$ (2.5 g per litre stock solution)	0.1
$ZnSO_4.7H_2O$ (2.9 g per litre stock solution)	0.1

Note: In Experiment No. 1 & 4, Fe was added as Fe-EDTA. In Experiment No. 5 & 6, Fe was added as Fe-EDDHA from a stock solution @ 4.0 mg l^{-1} to the nutrient solution in the pots to improve the iron availability to the plants under alkaline pH conditions

Appendix - B: Composition of Phostrogen Plant Food Material

Nutrients elements	Percentage
Total Nitrogen (N)	10.0
Nitric Nitrogen (N)	8.0
Ammonical Nitrogen (N)	2.0
Phosphorus Pentoxide (P_2O_5) soluble in Neutral Ammonium Citrate and Water	10.0 (P4.4%)
Phosphorus Pentoxide (P_2O_5) soluble in Water	10.0 (P4.4%)
Potassium Oxide (K_2O) soluble in Water	27.0(K22.4%)
Total Magnesium Oxide (MgO)	2.2 (Mg 1.3%)
Magnesium Oxide (MgO) soluble in Water	2.2 (Mg 1.3%)
Total Sulphur Trioxide (SO_3)	12.0(S 4.8%)
Sulphur Trioxide (SO_3) soluble in Water	12.0(S 4.8%)
Total Iron (Fe)	0.40
Iron (Fe) soluble in water	0.35
Total Manganese (Mn)	0.02
Manganese (Mn) soluble in Water	0.02
Calcium Oxide (CaO) soluble in Water	5.0 (Ca 3.6%)

Note: Phostrogen is produced in Great Britain by Phostrogen Ltd. Corwen, Clwyd, LL21 0EE

Appendix - 2.1: Analysis of variance for flag leaf area per plant in 4 wheat varieties at different salinity levels.

Source	DF	SS	MS	F	P
Plant age	2	220421	110210	28.83	0.000
Salinity	3	530676	176892	46.27	0.000
Variety	3	255245	85082	22.25	0.000
Age x salinity	6	247284	41214	10.78	0.000
Age x variety	6	64690	10782	2.82	0.012
Salinity x variety	9	26723	2969	0.78	0.638
Age x salinity x variety	18	67252	3736	0.98	0.488
Error	181	692034	3823		
Total	228				

Appendix - 2.2: Analysis of variance for length of main tillers in 4 wheat varieties at different salinity levels.

Source	DF	SS	MS	F	P
Salinity	3	2495.14	831.71	12.75	0.000
Variety	3	5352.73	1784.24	27.35	0.000
Salinity x variety	9	1050.50	116.72	1.79	0.077
Error	122	7958.44	65.23		
Total	137	16630.19			

Appendix - 3.1: Analysis of variance for flag leaf area in 6 wheat varieties at Pindi Bhattian

Source	DF	SS	MS	F	P
Variety	5	16.26	3.25	0.53	0.754
Site	1	1090.65	1090.65	176.64	0.000
Variety*Site	5	15.07	3.01	0.49	0.782
Error	24	148.18	6.17		
Total	35	1270.16			

Appendix - 4.1: Analysis of variance for flag leaf area in 10 wheat varieties at Sadhuke

Source	DF	SS	MS	F	P
Variety	9	22.029	2.448	0.86	0.570
Site	1	1358.124	1358.240	475.79	0.000
Variety*Site	9	19.819	2.202	0.77	0.643
Error	40	114.179	2.854		
Total	59	1514.150			

Appendix - 4.2: Analysis of variance for Pn in flag leaves in 4 wheat varieties

Source	DF	SS	MS	F	P
Variety	3	9.636	3.212	11.19	0.000
Site	1	68.614	68.614	239.02	0.000
Variety*Site	3	16.496	5.499	19.16	0.000
Error	16	4.593	0.287		
Total	23	99.340			

Appendix - 5.1: Analysis of variance for Pn in 5th leaves in the two wheat varieties

Source	DF	SS	MS	F	P
Variety	1	0.03	0.03	0.0	0.956
Stress	1	113.77	113.77	11.43	0.001
Lights	5	5221.97	1044.39	104.94	0.000
Variety*Stress	1	101.58	101.58	10.21	0.002
Variety*Lights	5	85.98	17.20	1.73	0.139
Stress*Lights	5	141.23	28.25	2.84	0.021
Variety*Stress*Lights	5	25.07	5.01	0.50	0.772
Error	72	716.56	9.95		
Total	95	6406.20			

Appendix - 5.2: Analysis of variance for sodium in 5th leaves in the two wheat varieties

Source	DF	SS	MS	F	P
Variety	1	16.86	16.86	1.27	0.281
Stress	1	1041.04	1041.04	78.57	0.000
Variety*Stress	1	12.39	12.39	0.94	0.353
Error	12	158.99	13.25		
Total	15	1229.29			

Appendix - 6.1: Analysis of variance for Pn in the 6th leaves in SARC-1 wheat variety

Source	DF	SS	MS	F	P
Stress	1	738.11	738.11	407.31	0.000
pH	1	269.38	269.38	148.65	0.000
Stress*pH	1	4.80	4.80	2.65	0.108
Error	76	137.72	1.81		
Total	79	1150.02			

Appendix - 7.1: Analysis of variance for Pn in the 6th leaves in LU26S and Punjab-85 wheat varieties.

Source	DF	SS	MS	F	P
Variety	1	55.207	55.207	5.89	0.017
Stress	1	344.057	344.057	36.72	0.000
pH	1	2.516	2.516	0.27	0.606
Variety*stress	1	0.435	0.435	0.05	0.830
Variety*pH	1	3.147	3.147	0.34	0.564
Stress*pH	1	11.929	11.929	1.27	0.262
Variety*stress*pH	1	9.400	9.400	1.00	0.319
Error	88	824.542	9.370		
Total	95	1251.230			

Appendix - 7.2: Analysis of variance for number of tillers per plant in the 6th leaves in LU26S and Punjab-85 wheat varieties at final harvest.

Source	DF	SS	MS	F	P
Variety	1	33.06	33.06	9.74	0.002
Stress	1	680.34	680.34	200.49	0.000
pH	1	0.84	0.84	0.25	0.620
Variety*stress	1	37.01	37.01	10.91	0.001
Variety*pH	1	9.51	9.51	2.80	0.096
Stress*pH	1	6.67	6.67	1.97	0.163
Variety*stress*pH	1	3.06	3.06	0.90	0.344
Error	136	461.50	3.39		
Total	143	1231.99			

Appendix - 7.3: Analysis of variance for Na^+ in the 6th leaves in LU26S and Punjab-85 wheat varieties.

Source	DF	SS	MS	F	P
Variety	1	87.5	87.5	8.17	0.005
Stress	1	16889.0	16889.0	1576.65	0.000
pH	1	64.2	64.2	6.00	0.016
Variety*stress	1	40.0	40.0	3.73	0.057
Variety*pH	1	19.0	19.0	1.77	0.187
Stress*pH	1	51.7	51.7	4.83	0.031
Variety*stress*pH	1	13.1	13.1	1.23	0.271
Error	88	942.6	10.7		
Total	95	18107.2			