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The separate or the combined effect of hypoxia and salinity on growth and ionic relations of four wheat varieties

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To evaluate hypoxic-salinity tolerance in wheat varieties, three Japanese varieties (Nourin-61, Chikugo Izumi and Shirasagi Komugi, relatively salt tolerant) and one Pakistani variety (Blue Silver, relatively salt sensitive) were grown under control, hypoxia, saline and hypoxic-saline conditions. The results suggested that relatively hypoxia and salt tolerant variety Nourin-61 was capable of producing the highest relative shoot yield under combined stress conditions. On the other hand, relatively sensitive variety to both hypoxia and salinity conditions, could not withstand harmful effects of combined stress. A more close correlation of plant growth characters between salinity and hypoxic-salinity than hypoxia and hypoxic-salinity indicated that varieties with higher salt tolerance would suffer less than varieties with higher hypoxia tolerance under combined stress conditions. And the balance of Na/K ratio in shoot tissues seems to be the major evaluation factor as the tolerant variety when salinity and hypoxia stress occur together.

Key words: *hypoxia, growth and ionic composition, salinity, salt tolerance, wheat varieties*

1 INTRODUCTION

High salinity and waterlogging (low oxygen in root zone) are major constraints in irrigated agriculture. The effects of high salinity on plant growth under adequate root zone aeration have been studied and reviewed extensively (e.g. Schatchman and Munns, 1992). Similarly plant performance under hypoxic or anoxic conditions has also been studied and reviewed widely (e.g. Huang et al., 1994; Biemelt, 1998). Under conditions of combined stress of salinity and hypoxia, plant growth is affected much more adversely because oxygen deficiency in root zone inhibits oxidative phosphorylation which consequently restricts energy available for ion pumps involved in excluding salts from the root (Barrett-Lennard, 1986; Drew and Lauchli, 1985). There are sufficient information regarding the performance of wheat plant under separate effects of salinity and waterlogging but very little published information is available for the combined effects of salinity and waterlogging despite the fact that both the stresses frequently occur simultaneously in irrigated agriculture in arid and semi-arid regions of the world

Hypoxia is wide spread in waterlogged soils and causes many direct adverse effects on wheat plants such as early leaf senescence, slower shoot growth, cessation of seminal root growth and decreased nutrient accumulation especially N, P, K, Ca and Mg in shoot (Trought and Drew, 1980;). Waterlogging may also restrict plant physiological performance by trigging oxygen deficiency in root zone and altering nutrient status by changing their availability to the plant. As rainfall is very high in Japan, therefore, breeding and selection programs for wheat varieties include the waterlogging tolerance of the varieties along with other favorable and desirable characteristics. Consequently, most of Japanese wheat varieties such as Nourin-61 and parent varieties of Shirasagi Komugi are reported to be moderately waterlogging tolerant (Yoshida, Y.,1977). In the meantime, the Japanese wheat varieties such as Nourin-61, Shirasagi Komugi and Chikugo Izumi clarified that the salt tolerance was relatively high in our different research (Kamboh,A.M., 1999).

In the present paper, we planned to evaluate the effect of NaCl on the growth and the ionic relations of some Japanese wheat varieties which proved to be relatively salt tolerant and one Pakistani wheat variety, relatively salt sensitive one, with roots maintained under aerated or

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hypoxic conditions in solution culture. The object was to obtain some information on the response of different wheat varieties to the separate or the combined effect of hypoxia and salinity.

2 MATERIALS AND METHODS

Seeds of three Japanese wheat varieties (Nourin-61, Chikugo Izumi and Shirasagi Komugi) and one Pakistani wheat variety (Blue Silver) were germinated in the dark at 25°C in an incubator on double layer of filter papers moistened with distilled water in 90 mm petri dishes. Six days old plants were transplanted into plastic containers at the rate 40 plants per container by inserting plants into the holes of polystyrene sheet (1.5 cm thick) holding them in position by foam collars. The plastic containers contained 7 liter of 5% Hoagland's solution (having nutrient composition as given in Table 1). The solution was well aerated with two air curtains attached to air pump. The containers were placed on an elevated bench in a glass house where temperature prevailed at a maximum of 30°C during the day and a minimum of 12°C during the night throughout the growth period. Nutrient solution was replaced at a three-day interval. After nine days of plant growth under normal nutrient solution conditions, salinity and hypoxic stresses were imposed as detailed in Table 1.

Each variety contained ten plants per container (treatment) and each treatment was replicated twice. At the expiry of a further plant growth of nine days under various stress conditions, chlorophyll content of third leaf of each plant was recorded with a chlorophyll meter (Model SPAD-502, Minolta Camera Co. Ltd., Japan) before harvesting the plants. After harvesting, the plants were separated into root and shoot portions, thoroughly washed in three replacements of distilled water, blotted dry with tissue paper and root and shoot length and fresh weight were recorded. Root and shoot samples were dried at 80°C for two days in an oven before recording root and shoot dry weight. Oven-dried samples were ground and ashed in a muffle furnace at 500°C and contents were dissolved in HCl (1:1) on hot plate at 80°C by the procedure given by Ishihara (1975). Calcium, Magnesium, Potassium and Sodium contents were determined by Polarized Zeeman Atomic Absorption Spectrophotometer (Model Z-6100, Hitachi Ltd.).

Statistical analysis of the data was carried out by analysis of variance using SAS statistical computer software package and comparison of all pairs of treatments was conducted by Scheffe's test. And correlation analysis of the data such as plant growth parameters and nutritional status of four wheat varieties under hypoxia, saline and hypoxic-saline conditions was also carried out.

3 RESULTS

3.1 Effect of hypoxia, salinity and hypoxic-salinity on plant growth of wheat varieties

Table 1 Composition of treatments.

Control solution					
Macro-nutrients (ppm)			Micro-nutrients (ppm)		
NH_4-N	5.0	NH_4NO_3	Fe	0.31	EDTA-$Fe.2H_2O$
NO_3-N	5.0	NH_4NO_3	Mn	0.025	$MnSO_4.5H_2O$
P	1.6	$Na_2HPO_4.12H_2O$	B	0.025	H_3BO_3
K	10.0	KCl	Zn	0.035	$ZnSO_4.7H_2O$
Ca	10.3	$CaCl_2.2H_2O$	Cu	0.03	$CuSO_4.5H_2O$
Mg	2.4	$MgSO_4.7H_2O$	Mo	0.025	$H_2MoO_4.H_2O$
Treatments					
Control	Well aerated nutrient solution				
Hypoxia	Stagnant nutrient solution				
Saline	Well aerated nutrient solution containing 100 mM NaCl				
Hypoxic-saline	Stagnant nutrient solution containing 100 mM NaCl				

Table 2 Effect of hypoxic, salinity(100 mM NaCl) and hypoxic-salinity stress for 9 days on plant growth parameters of Nourin -61, Chikugo Izumi, Shirasagi Komugi and Blue Silver varieties of wheat. Values in ( ) are % of respective controls.

Variety	Control		Hypoxia			Saline			Hypoxic- saline		
Root Length (mm)											
Nourin-61	603.6±5.6	a	351.0±12.2	(58)	b	344.8±9.2	(57)	b	250.6±5.2	(42)	c
Chikugo Izumi	623.1±5.6	a	393.7±9.5	(63)	b	291.9±6.6	(47)	c	245.3±7.1	(39)	d
Shirasagi Komugi	666.2±10.3	a	375.5±6.6	(56)	b	378.4±6.1	(57)	bc	266.7±7.4	(40)	d
Blue Silver	614.2±6.9	a	355.9±7.2	(58)	b	264.1±4.5	(43)	c	196.6±10.2	(32)	d
Shoot Length (mm)											
Nourin-61	301.6±6.2	a	298.7±8.0	(99)	a	261.8±6.6	(87)	b	235.0±6.8	(78)	b
Chikugo Izumi	311.6±7.7	a	308.7±7.2	(99)	a	240.9±6.0	(77)	b	231.3±5.8	(74)	b
Shirasagi Komugi	312.8±7.7	a	297.1±5.2	(95)	a	263.7±5.8	(84)	b	230.6±6.8	(74)	c
Blue Silver	310.6±4.5	a	292.3±8.6	(94)	a	226.0±6.2	(73)	b	202.7±6.8	(65)	c
Root Dry Weight (mg plant^{-1})											
Nourin-61	114.2±3.0	a	94.5±0.8	(83)	b	64.4±1.7	(56)	c	55.7±1.2	(49)	d
Chikugo Izumi	112.4±2.1	a	93.4±1.5	(83)	b	54.1±1.2	(48)	c	38.5±0.7	(34)	d
Shirasagi Komugi	112.5±1.4	a	79.8±1.2	(71)	b	66.5±1.4	(59)	c	50.9±1.2	(45)	d
Blue Silver	74.0±1.6	a	60.3±1.7	(82)	b	39.1±1.9	(53)	c	32.7±0.9	(44)	c
Shoot Dry Weight (mg plant^{-1})											
Nourin-61	177.4±3.5	b	199.7±2.5	(113)	a	132.5±1.2	(75)	c	119.6±1.5	(67)	d
Chikugo Izumi	166.1±2.5	b	180.7±1.2	(109)	a	106.9±1.9	(64)	c	93.7±1.2	(56)	d
Shirasagi Komugi	166.0±1.6	a	158.4±1.2	(95)	b	127.6±1.1	(77)	c	91.3±0.9	(55)	d
Blue Silver	167.6±1.8	a	142.6±1.4	(85)	b	91.2±1.1	(54)	c	77.3±1.3	(46)	d
Root/Shoot Ratio (dry weight)											
Nourin-61	0.64±0.02	a	0.47±0.01	(72)	b	0.49±0.01	(75)	b	0.47±0.01	(72)	b
Chikugo Izumi	0.68±0.02	a	0.52±0.01	(76)	ab	0.51±0.01	(75)	ab	0.41±0.01	(61)	c
Shirasagi Komugi	0.68±0.02	a	0.50±0.01	(74)	c	0.52±0.01	(77)	c	0.56±0.02	(82)	b
Blue Silver	0.44±0.01	a	0.42±0.01	(96)	b	0.43±0.02	(97)	ab	0.42±0.01	(96)	b
Chlorophyll Content											
Nourin-61	40.5±0.8	a	38.3±0.7	(95)	b	40.7±0.7	(101)	a	38.0±0.4	(94)	b
Chikugo Izumi	38.0±0.9	a	34.2±0.8	(90)	b	35.2±0.8	(93)	ab	27.1±1.4	(71)	c
Shirasagi Komugi	37.7±1.3	a	38.8±0.8	(103)	a	39.1±0.5	(104)	a	28.2±1.1	(75)	b
Blue Silver	35.0±0.4	a	34.7±0.5	(99)	a	31.3±0.5	(89)	a	17.9±1.7	(51)	b

Different letters within row for a specific plant growth parameter indicate a significant difference at the 1% level. according to Scheffe's test

Statistical analysis of data showed considerable differences in the response of the various wheat varieties to hypoxic, saline or hypoxic-saline stress in terms of significant reduction in different plant growth characters. In general, hypoxic or saline stress reduced plant growth and the detrimental effects of these stresses were further aggravated when they occur together (Table 2).

3.1.1 Root and shoot length

Under hypoxic conditions, 37-44% reduction in root length and a negligible (1-6%) reduction in shoot length of all the varieties was recorded. The difference in root length among treatments significantly occurred in all varieties, however, there was no significance in shoot length between saline and hypoxic-saline stress on Nourin 61 and Chikugo Izumi while Pakistani wheat variety, Blue Silver showed relatively much reduction in root and shoot length under hypoxic-saline conditions.

3.1.2 Root and shoot dry weight

The difference in root and shoot dry weight among treatments significantly occurred in all varieties, however, the reaction was different by each wheat variety. As regards shoot dry weight, Nourin-61 and Chikugo Izumi proved hypoxic favoring and showed no reduction rather slight increase under hypoxic conditions. Under saline conditions, Nourin-61 and Shirasagi Komugi were more tolerant while Blue Silver was the most sensitive in terms of shoot dry weight. However, under hypoxic-saline condition, Shirasagi Komugi failed to maintain its shoot growth and behaved as moderately tolerant along with

Chikugo Izumi while Nourin-61 was most tolerant and Blue Silver was most sensitive.

3.1.3 Root/shoot ratio (dry weight)

The analysis of root/shoot ratio (dry weight) data revealed that almost similar pattern of response was observed in Nourin-61 and Blue Silver under hypoxic, saline and combined conditions while the values of Chikugo Izumi and Shirasagi Komugi under combined stress of hypoxia and salinity were different significantly among the other treatments.

3.1.4 Leaf chlorophyll content

As regards Nourin-61, there was no effect of salinity stress on leaf chlorophyll content whereas the reduction under combined stress of salinity and hypoxia was identical to hypoxia stress alone. Furthermore, this reduction was very little (only 6%) in Nourin-61 than all other varieties exhibiting 25-50% reduction compared to respective controls. In the meantime, Chikugo Izumi, Shirasagi Komugi and Blue Silver showed no significant reduction in leaf chlorophyll contents under hypoxic or saline conditions but failed to maintain it under combined stress conditions exhibiting a considerable decrease. The reduction was much higher in Blue Silver than the other varieties.

3.2 Effect of hypoxia, salinity and hypoxic-salinity on ionic composition of roots and shoots of various wheat varieties

3.2.1 Sodium

Sodium content of root were increased by hypoxic stress in all varieties, the increase being the lowest and non-significant in Nourin-61 and the highest and highly significant in Blue Silver. Similarly salinity stress also increased Na content of root significantly in all varieties and accumulation of Na in roots was further aggravated in all varieties under combined stress except Nourin-61 (Fig. 1).

Na content of shoot were increased under salinity and hypoxic-saline stress conditions in all varieties, however, there was non-significant increase in all varieties under hypoxic stress conditions. Shirasagi Komugi and Nourin-61 showed lower accumulation of Na in shoots under saline or hypoxic-saline stress conditions compared to Chikugo Izumi and Blue Silver. Especially Nourin-61 proved to be capable of maintaining lower Na content of shoot under these conditions compared to all other varieties.

3.2.2 Potassium

Hypoxic stress did not reduce K content of root in all varieties. Salinity resulted in significant increase in K content of root in all varieties except Chikugo Izumi, and in non-significant decrease between salinity and combination of both stresses except Nourin-61 (Fig. 1).

The effect of hypoxic stress was statistically non-significant on shoot K content of shoot in all varieties except Shirasagi Komugi while salinity stress reduced K content significantly compared to their respective control. The reduction effect was further aggravated by combination of both stresses in all varieties. However, Nourin-61 was capable of maintaining the highest K content of shoot or the lowest reduction among all varieties even under combination of both stresses (Fig. 1).

3.2.3 Calcium

Hypoxia and salinity caused significant reduction in Ca content of root in all varieties compared to their respective controls. However, the loss was much higher by salinity than hypoxia in all varieties. Although combined stress of hypoxia and salinity resulted in higher Ca loss in root than salinity or hypoxic stress alone but the loss was non significant in all Japanese varieties compared to salinity stress while such loss highly significant in Blue Silver (Fig. 2).

Hypoxic stress reduced Ca content of shoot of Nourin-61 and Chikugo Izumi, increased of Blue Silver while unaffected that of Shirasagi Komugi. Salinity stress reduced Ca content of shoot of all varieties and combined stress also reduced significantly Ca content of shoot of Chikugo Izumi and Shirasagi Komugi compared to respective salinity stress except Nourin-61 which experienced an improvement, although non significant, in Ca content of shoot (Fig.2).

3.2.4 Magnesium

Hypoxia, salinity and combination of both stresses brought significant reduction in Mg content of root of all varieties compared to respective controls. However, Mg content of root of Chikugo Izumi and Shirasagi Komugi was statistically alike under salinity and combination of both stresses (Fig.2).

As regards shoot Mg content, hypoxic stress did not affect in Nourin-61 and Chikugo Izumi, reduce significantly in Shirasagi Komugi and increase in Blue Silver. Salinity stress reduced Mg content of shoot in all varieties. The combination of salinity and hypoxia decreased Mg content of shoot of Shirasagi Komugi, did not affect of Nourin-61, Chikugo Izumi, and increased in

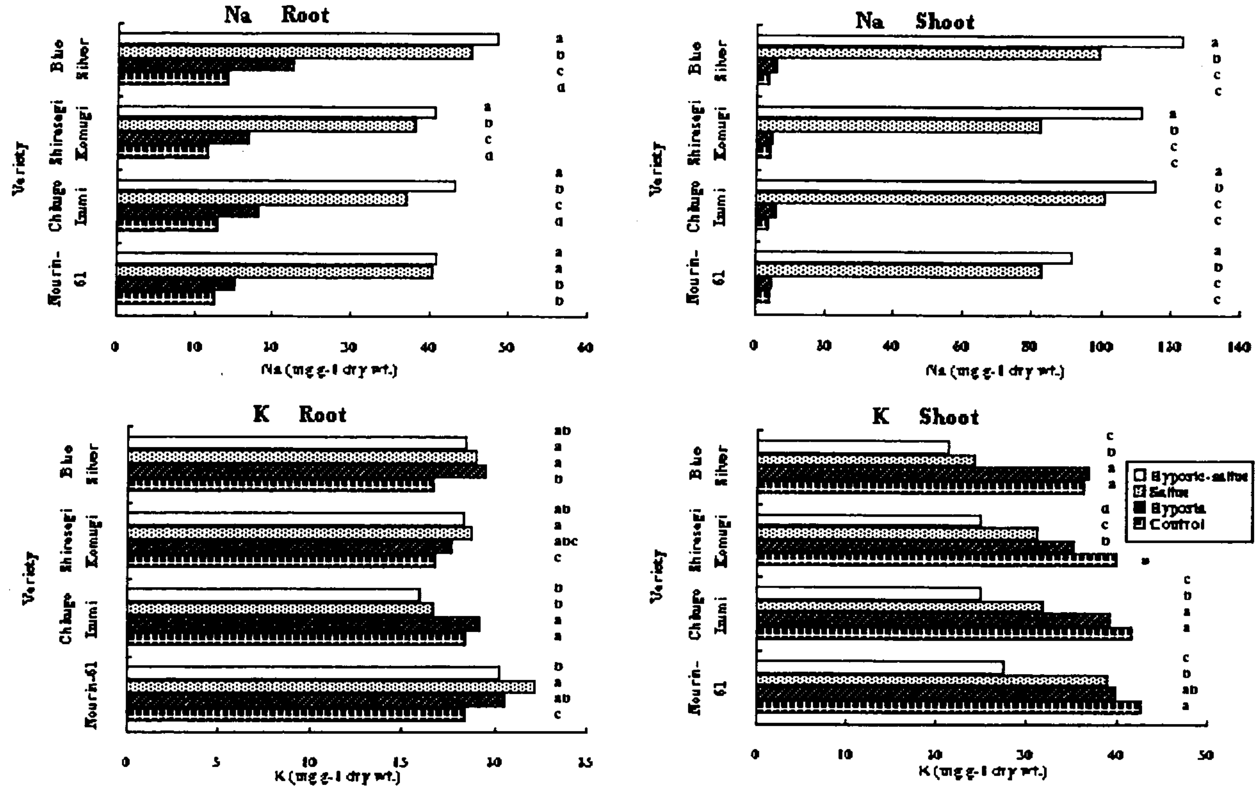

Fig. 1. Effect of hypoxia, salinity and hypoxic-salinity stress for 9 days on sodium (Na) and potassium(K) content of roots and shoots of Nourin-61, Chikugo Izumi, Shirasagi Komugi and Blue Silver varieties of wheat. Different letters within figure among each treatments indicate a significant difference at the 1% level according to Sheffe's test.

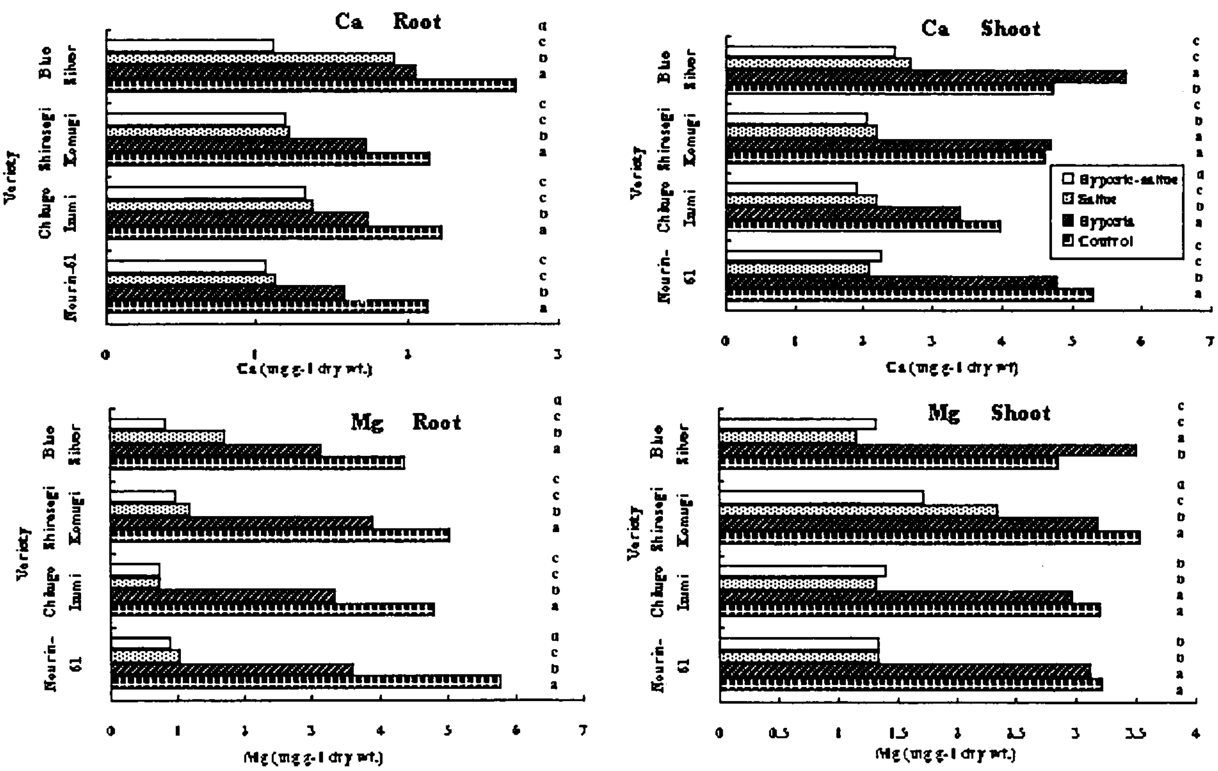

Fig. 2. Effect of hypoxia, salinity and hypoxic-salinity stress for 9 days on calcium (Ca) and magnesium (Mg) content of roots and shoots of Nourin-61, Chikugo Izumi, Shirasagi Komugi and Blue Silver varieties of wheat. Different letters within figure among each treatments indicate a significant difference at the 1% level according to Sheffe's test.

Blue Silver non significantly compared to respective salinity stress alone (Fig. 2).

3.2.5 Na/K ratio and Na/Ca ratio

Hypoxic stress increased the Na/K ratio of root of all varieties. However, the increase was significant and alike for Chikugo Izumi, Shirasagi Komugi and Blue Silver whereas negligible and non-significant for Nourin-61. Similarly Na/K ratio of root was also increased by salinity and by hypoxic-salinity stress. The percent increase was much lower in Nourin-61 compared to all other varieties under saline or hypoxic-salinity stress (Fig.3).

Na/K ratio of shoot was increased significantly by salinity stress and non significant increase by hypoxic stress in all varieties. This increase was further enhanced combined stress. Nourin-61 showed its capability to maintain the lowest percent increase while Blue Silver experienced the highest increase in Na/K ratio of shoot among all varieties under saline or hypoxic-salinity stress (Fig.3).

All the varieties behaved similarly for Na/Ca ratio of root and shoot under hypoxic stress as in case of Na/K ratio. However, statistical analysis of the data revealed that when hypoxic stress combines with salinity stress, the Na/Ca ratio in roots and shoots increased significantly in all varieties except in Nourin-61 compared to salinity stress alone.

4 DISCUSSION

Hypoxia and salinity reduced the root length significantly in all varieties. The effect of hypoxia or salinity alone was equivalent and alike in Nourin-61 and Shirasagi Komugi but combination of both stresses brought a further reduction in root length. In contrast, the effect of hypoxia alone was relatively less than salinity stress alone in Chikugo Izumi and Blue Silver but combination of both stresses resulted in more reduction in root length than the effect of both stresses separately. Although hypoxic stress affected shoot length negligibly in all varieties, its occurrence along with salinity stress caused reduction in shoot length much more than salinity stress alone. These results are in agreement with those reported by Huang et al. (1994). Blue Silver was similar

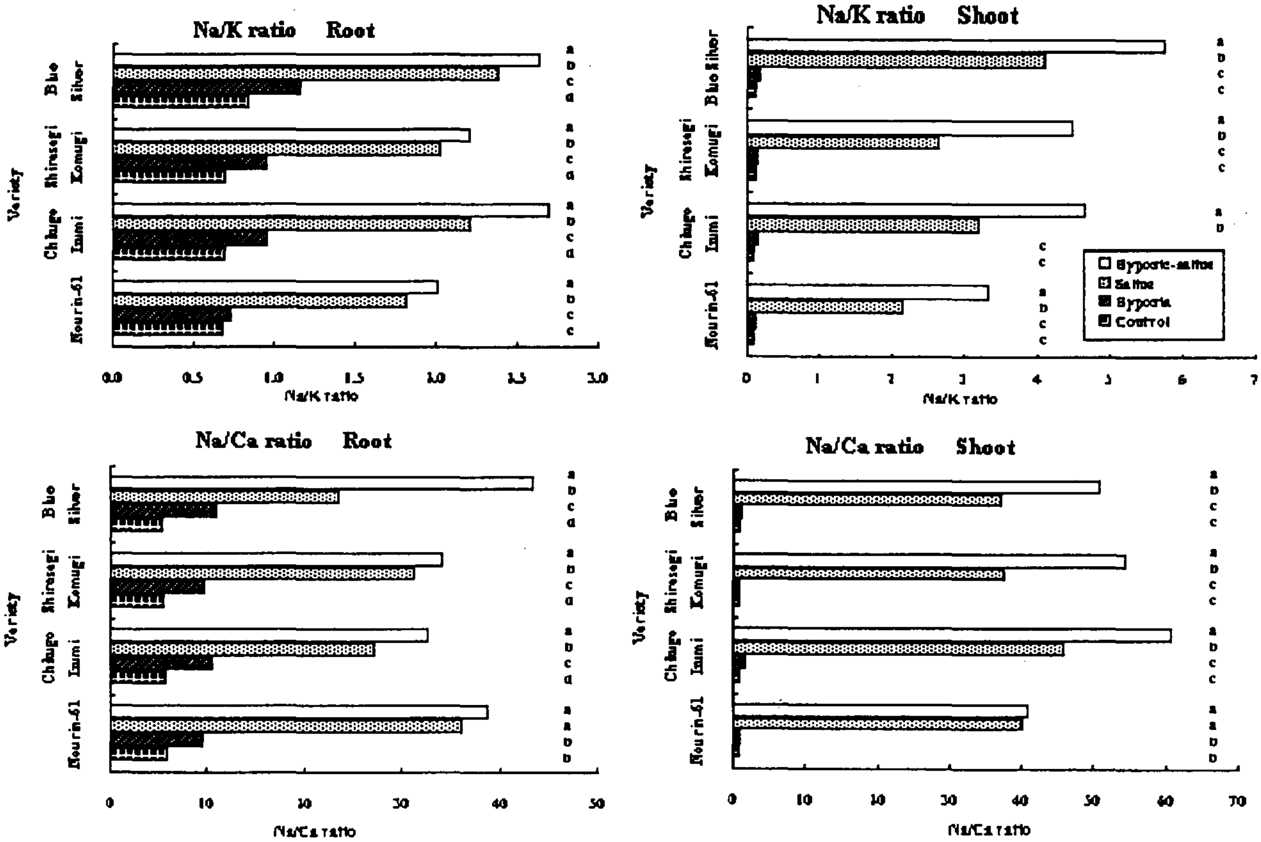

Fig. 3. Effect of hypoxia, salinity and hypoxic-salinity stress for 9 days on Na/K and Na/Ca ratio in roots and shoots of Nourin-61, Chikugo Izumi, Shirasagi Komugi and Blue Silver varieties of wheat. Different letters within figure among treatments indicate a significant difference at the 1% level According to Scheffe's test.

to Nourin-61 in response to hypoxia stress on root length. Being a salt sensitive variety, Blue Silver could not withstand the harmful effects of combined stress and showed the highest reduction in root growth. It was due to cessation of root elongation, failure to produce enough adventitious roots and its inefficiency to avoid the nutrient imbalance and Na toxicity.

Hypoxic stress clearly aggravated inhibitory effects of salinity stress on shoot growth. Japanese varieties were sufficiently hypoxia tolerant and exhibited no major reduction in shoot growth rather shoot growth was slightly improved in some varieties while Pakistani wheat variety showed significant decrease in shoot weight proving to be relatively hypoxia sensitive variety. Hypoxia is reported to reduce shoot growth more sensitive varieties through its adverse effects on root aerobic respiration and disruption in translocation of root produced metabolites to shoots as well as increased accumulation of toxic ions (Reid and Bradford, 1984). Salinity and hypoxia occurring together cause damage in excess of that found with either salinity or hypoxia alone because accumulation of Na under salinity is further aggravated by the hypoxic stress. Though in our experiment, Na contents in the root of most varieties increased by the hypoxia stress only compared to the control, this phenomenon seems to be occurred due to hypoxia-induced adverse effects on Na efflux, increased permeability of root membranes to Na and root disorganization allowing Na entrance by appoplastic pathway as Barrett-Lennard et al.(1999) reported.

The leaf chlorophyll content were not much affected by hypoxia in almost all varieties as also reported by Thomson et al. (1992) who observed loss in chlorophyll contents only after prolonged waterlogging stress. Hypoxia combined with salinity intensified the chlorophyll loss in all varieties except Nourin-61. Blue Silver was affected much more (50% loss) probably due to enhanced Na accumulation in shoots causing premature senescence.

Na accumulation in roots and shoots of Nourin-61 was non-significantly higher under hypoxic stress compared to control. All other varieties experienced significant Na accumulation in roots.

Potassium contents of shoot were strongly depressed by salinity stress in agreement with other earlier reports (Gorham et al., 1984). All varieties except Chikugo Izumi, accumulated higher quantities of K in roots under hypoxia, salinity or hypoxic-salinity conditions probably due to disorganization of the roots under stress conditions. It was revealed that even higher uptake of K by roots especially in sensitive variety, could not enable to maintain K content in shoots due to impairment of K transport. Although it is reported that cereal roots have higher selectivity for transport of K over Na (Jeschke, 1984), the excess of Na over K may displace K from selective sites on carriers or channels that are essential in energy dependent influx. Hypoxia resulted in passive influx of Na and arrested K transport to shoots, consequently Na/K ratio in the shoots was increased many times especially in sensitive variety Blue Silver.

It can be concluded that a variety tolerant to salinity may be expected to perform well under combined stress of salinity and hypoxia as plant performance under these stress conditions is determined by plant K, Ca and Na contents and their ratios especially in shoots, and salinity affects these contents much more than hypoxia stress. Also the degree of hypoxia tolerance of salt tolerant variety may be helpful in avoiding aggravative adverse effects of combined stress of salinity and hypoxia.

5 CONCLUSION

The results of this study exhibited that hypoxic stress aggravates the effects of salinity stress on plant growth under combined stress conditions. However, the wheat varieties with higher salt tolerance suffer less than varieties with higher hypoxia tolerance when both stresses occur together. Also the degree of hypoxia tolerance of salt tolerant variety was much contributing in avoiding aggravating effects of hypoxia under saline conditions. On the other hand, the balance of Na/K ratio in shoot tissues seems to be the major evaluation factor as the tolerant variety when salinity and hypoxia stress occur together.

Our study suggested that Nourin-61, being a salt tolerant variety, seemed to be capable of effective Na exclusion. Thus it allowed sufficient absorption of K, and transported it to shoot to keep higher K content and lower Na/K ratio in shoot for proper plant growth under combined stress conditions. In contrast, relatively salt sensitive Blue Silver could not restrict free Na flux into roots and consequently in shoot leading to higher Na content and Na/K ratio in shoot resulting in poor growth. Concerning other two varieties, Shirasagi Komugi seems to be more salinity tolerant variety than Chikugo Izumi while the hypoxia tolerance shows the reverse relation. Shirasagi Komugi, however, was similar to in response to Chikugo Izumi under combined stress on their growth. We need more information on Na exclusion capability and K selectivity of these two varieties.

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