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Full Length Research Paper

Differential effects of aluminium on the seedling parameters of wheat

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In order to determine the effect of different aluminium (Al) concentrations on the seedling parameters of wheat and the effect of malate and citrate treatments as chelates for reducing the noxious effect of Al in medium culture and seedlings of two wheat cultivars, Darab (Al sensitive) and Maroon (Al tolerant) were grown on hydroponic solution (non modified Hoagland) containing $AlCl_3$ (0-100-200-300 µM). Factorial experiment was realized in a complete randomized design with three replications. The root and shoot length as well as fresh and dry weight of roots and shoots were measured. Leaf area was measured by a special computer program named compuEyeLSA. Analysis of variance (ANOVA) revealed that, for fresh weight of root (FWR), fresh weight of shoot (FWS), dry weight of shoot (DWS) and length of root (LR), the main effect of genotype, Al concentration and their interaction was highly significant, whereas, in the case of dry weight of root (DWR) and leaf area (LA) traits, only the main effect of genotype and Al concentration were highly significant. LS trait only was affected by different Al concentrations. ANOVA indicated a significant interaction between genotype and Al concentration for DWS, FWR, FWS and LR traits. Therefore, a separate regression analysis was conducted for each genotype. We found difference in fitted model between two studied varieties. In the second experiment the effect of malate and citrate treatments was studied on reducing the noxious effect of Al in medium culture. ANOVA revealed that, there are significant differences among applied treatments on studied seedling growth parameters. This means that the application of malate or citrate is effective in some Al concentrations as compared to others.

Key words: *Triticum aestivum* L., hydroponic, aluminium-tolerant, length of root, regression analysis.

INTRODUCTION

Phytotoxic aluminium (Al) ion (mainly Al^{3+}) restricts crop productivity in acidic soils that cover almost 40% of world's arable land (Foy, 1988; Kochian, 1995; Matsumoto, 2000; Kochian et al., 2004). While acid soils present a number of challenges to plant growth, the major limit to production is Al toxicity, since micromolar concen-trations of the trivalent Al cations can rapidly inhibit root growth (Foy et al., 1978; Carver and Ownby, 1995). Al toxicity inhibits root cell division and elongation, thus reducing water and nutrient uptake, consequently resulting in poorer plant growth and yield (Alam, 1981; Clarkson, 1966; Foy, 1983; Foy et al., 1967; Gauthier, 1953; Reid et al., 1969). Relative shoot and root dry weights in tolerant barley cultivars was two and three fold respec-tively compared to susceptible cultivars (Foy, 1996). Root elongation is affected within hours of Al exposure (Wallace et al., 1982), and as in many plant species, the primary site of Al toxicity in wheat (*Triticum aestivum* L.) appears to be

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Abbreviations: DWS, Dry weight of shoot; **DWR,** dry weight of root; **FWR,** fresh weight of root; **FWS,** fresh weight of shoot; **LR,** length of root; **LS,** length of shoot; **LA,** leaf area.

the root apex (Bennet and Breen, 1991). Ryan and Kochian (1993) have shown that in wheat and maize, root elongation is inhibited only when apices are exposed to Al, whereas selectively exposing the remainder of the root does not inhibit elongation.

Many plants have evolved mechanisms to tolerate aluminum stress and there is a significant variation in Al tolerance within some species, such as wheat and maize (Kochian et al., 2004). Control of rhizosphere pH has been proposed as a means of Al avoidance, because aluminum solubility is very pH dependent (Foy, 1988; Foy et al., 1965; Taylor, 1987). Aluminum tolerance in wheat, barley, rye and triticale is associated with an increased pH of the growth medium (Foy et al., 1965; Mugwira and Patel, 1977) or an increased resistance towards lowering the pH of a mixed $NH4^+/NO3^-$ solution (Taylor, 1987; Foy, 1985). However, there is a controversy surrounding the observed pH difference that is, if it is the cause or the effect of differential Al tolerance. Wagatsuma and Yamasaku (1985), found no positive correlation between aluminum tolerance in barley and pH changes in the bulk nutrient solution induced by the plant in response to manipulation of nitrogen (N) sources. Taylor (1988) found similar results for winter wheat. Al tolerance in some wheat cultivars is inherited in a simple manner consistent with the presence of a major dominant gene conferring Al tolerance (Kerridge and Kronstad, 1968; Larkin, 1987). Other cultivars show a more complex inheritance, indicating the presence of several additive genes (Aniol, 1991).

In some plants, the increased secretion of organic acids is localized in the root apex and depends upon the presence of Al in the external solution (Kollmeier and Horst, 2001; Ma et al., 2001; Zhang et al., 2001). The root apex is particularly sensitive to Al, therefore only the cat-ions those immediately surrounding the apical root cells need to be detoxified. It has been showed that, the organic acids protect the root apex from the toxic Al cations by forming chelates with Al. In this study, we observed: effect of different Al concentrations on the seedling parameters of two wheat cultivars, and the effect of malate and citrate treatments as chelates on reducing the noxious effect of Al in medium culture.

MATERIALS AND METHODS

Plant materials and experimental design

The seeds of two wheat cultivars, Darab (Al sensitive) and Maroon (Al tolerant) were prepared from Agricultural Research Center of Karaj. The seeds of two cultivars were sterilized with 5% (v/v) sodium hypochlorite for 15 min then were rinsed with distilled H_2O for 15 min and were kept in the dark for 24 h at 25°C. Germinated seeds were placed on a plastic net, which was floated on a continuously aerated solution containing 0.5 mM $CaCl_2$. The seedlings were kept in the dark for 1 day at 25°C and then, were moved to natural light. Solution was renewed daily and seedlings were selected for treatment by measuring uniform root length. Pre-culture solution were replaced by hydroponic solution (non modified Hoagland) containing $AlCl_3$ (0-100-200-300 µM) and pH was kept constant at 4. Factorial experiment was realized in a complete randomized design with three replications. Each replication consisted of one Petri dish of ten seedlings per cultivar and $AlCl_3$ combinations. Treatment solutions were renewed every 3 days with fresh solution (Zakir et al., 2005). The plants were grown for 15 days under a 16 h photoperiod. The 15 days old plants used for the experiments for in citrate and malate used as phytochelator for decreasing the effect of aluminum toxicity.

Measurement of root, shoot and leaf area

At the end of the treatment application (after 15 days), root and shoot length was measured after washing in distilled water and using a digital scale (Metler) with 0.001 g sensitivity. Fresh weight of roots and shoots was also determined. Leaf area was measured by a special computer program named compuEyeLSA (leaf & symptom area by Dr Ehab M. Baker). The samples were put in oven with 80°C for 48 h then the dry weight of roots and shoots was determined.

Data analysis

Analysis of variance (ANOVA) was performed using the general linear model (GLM) procedure in the SAS software (SAS Institute Inc., Cary, NC, USA). The main effect of genotype and Al concentration as well as their interactions was determined. To generate a trend analysis, the Proc REG procedure of PC-SAS is specified (SAS Institute Inc., Cary, NC, USA). Commands for each model are placed after the Proc Reg statement. A separate model statement is required for linear, quadratic and cubic trends.

RESULTS

ANOVA revealed that, for seedling growth parameters such as dry weight of shoot (DWS), fresh weight of root (FWR), fresh weight of shoot (FWS) and length root (LR) the main effect of genotype, Al concentration and their interactions was highly significant, whereas in the case of dry weight of root (DWR) and leaf area (LA) traits just the main effect of genotype, Al concentration was highly significant. Length shoot (LS) only was affected by different Al concentrations (Table1).

As shown in Figure 1, for DWR there was significantly difference between Maroon and Darab in all Al concentrations. On the other hand, by increasing the amount of aluminum concentration in medium culture DWR was significantly decreased. In the case of LS trait, we did not find any difference between the genotypes in all Al concentrations but it was affected by the amount of aluminum concentration in medium culture so that by increasing Al concentration it decreased in the both genotypes in similarly trend.

ANOVA indicated a significant interaction between genotypes and Al concentrations for DWS, FWR, FWS and LR traits. Therefore, a separate regression analysis was conducted for each genotype. Response of Maroon and Darab DWS, best fit the linear model as indicated by a significant T-value (Table 2). However, the regres-sion equations differed for each genotype (Y = 0.312 -

Table 1. Analysis of variance summary for wheat seedling growth parameters data, under different Al concentrations. Data were analyzed using procedures for a completely randomized design.

Source	df	Mean of square						
		DWR	DWS	FWR	FWS	LS	LA	LR
Line	1	0.003**	0.004**	0.26**	0.09*	2.331ns	19.62**	35.50**
Al concentration	3	0.001**	0.014**	0.61**	1.40**	40.569**	45.96**	205.30**
Line ×Al concentration	3	0.000005ns	0.002**	0.05**	0.07*	0.850ns	0.27ns	2.68*
Error	16	0.00002	0.00008	0.006	0.015	0.833	0.11	0.802
C.V.		6.66		10.92	7.03		3.68	3.75

df, Degrees of freedom; **, *, Significant at 0.01 and 0.05 probability level; ns, non significant.

Table 2. Summary table for wheat seedling growth parameters in different Al concentrations using regression analysis.

Character	Line	Source	Linear				Quadratic				Cubic			
			Pr>(T)	R^2	Estimate	SE	Pr>(T)	R^2	Estimate	SE	Pr>(T)	R^2	Estimate	SE
DWR	R	Intercept	-	-	0.09	0.00201	-	-	0.09	0.00241	-	-	0.09	0.00253
		Concentration	***	0.92	-0.00012	0.00001	***	-	-0.0001	0.00004	ns	-	-0.0002	0.000097
		$Concentration^2$	-	-	-	-	ns	0.91	8.33	1.237031E-7	ns	-	7.33	8.590208E-7
		$Concentration^3$	-	-	-	-	-	-	-	-	ns	0.91	-1.44	1.888072E-9
	S	Intercept	-	-	0.06	0.00195	-	-	0.07	0.00204	-	-	0.06	0.00191
		Concentration	***	0.91	-0.00011	0.00001	***	-	-0.0002	0.000033	***	-	-0.0003	0.000073
		$Concentration^2$	-	-	-	-	ns	0.93	1.92	1.048882E-7	ns	-	0.000001	6.493587E-7
		$Concentration^3$	-	-	-	-	-	-	-	-	ns	0.94	-2.38889E-9	1.427248E-9
DWS	R	Intercept	-	-	0.312	0.00752	-	-	0.302	0.00623	-	-	0.30	0.00635
		Concentration	***	0.93	-0.0005	0.00004	ns	-	-0.0002	0.0001	ns	-	0.00004	0.00024
		$Concentration^2$	-	-	-	-	**	0.97	-0.000001	3.194807E-7	ns	-	-0.000003	0.0000022
		$Concentration^3$	-	-	-	-	-	-	-	-	ns	0.97	5E-9	4.732016E-9
	S	Intercept	-	-	0.25	0.00321	-	-	0.25	0.00387	-	-	0.25	0.00332
		Concentration	***	0.94	-0.00025	0.00002	***	-	-0.0003	0.00006	**	-	-0.0005	0.00013
		$Concentration^2$	-	-	-	-	ns	0.95	1.166667E-7	1.983108E-7	ns	-	0.000003	0.000001
		$Concentration^3$	-	-	-	-	-	-	-		ns	0.96	-5.44444E-9	2.475185E-9
FWR	R	Intercept	-	-	1.28	0.06719	-	-	1.38	0.05576	-	-	1.39	0.05294
		Concentration	***	0.87	-0.003	0.00036	***	-	-0.006	0.0009	**	-	-0.009	0.00203

Table 2: Contd.

		Concentration^2	-	-	-	-	***	0.93	0.000009	0.000003	ns	-	0.00004	0.00002
		Concentration^3	-	-	-	-	-	-	-	-	ns	0.94	-6.25E-8	3.946244E-8
		Intercept	-	-	0.87	0.03117	-	-	0.90	0.03274	-	-	0.90	0.03519
	S	Concentration	***	0.91	-0.02	0.0002	***	-	-0.003	0.00053	*	-	-0.003	0.00135
		Concentration^2	-	-	-	-	ns	0.92	0.0000031	0.000002	ns	-	0.0000083	0.000012
		Concentration^3	-	-	-	-	-	-	-	-	ns	0.92	-1.16667E-8	2.623258E-8
	R	Intercept	-	-	2.31	0.07610	-	-	2.28	0.09228	-	-	2.25	0.08221
		Concentration	***	0.91	-0.004	0.00041	*	-	-0.004	0.00148	ns	-	0.002	0.00315
		Concentration^2	-	-	-	-	ns	0.90	-0.000002	0.000005	ns	-	-0.00006	0.000028
		Concentration^3	-	-	-	-	-	-	-	-	ns	0.92	1.215556E-7	6.127831E-8
		Intercept	-	-	2.28	0.05718	-	-	2.25	0.06723	-	-	2.28	0.05606
FWS	S	Concentration	***	0.91	-0.003	0.00031	ns	-	-0.002	0.00108	*	-	-0.007	0.00215
		Concentration^2	-	-	-	-	ns	0.91	-0.000003	0.0000035	ns	-	0.00004	0.00002
		Concentration^3	-	-	-	-	-	-	-	-	*	0.94	-9.91111E-8	4.178225E-8
		Intercept	-		31.46	0.62262	-	-	31.85	0.72134	-	-	32.12	0.66145
	R	Concentration	***	0.74	-0.02	0.00333	*	-	-0.031	0.01158	*	-	-0.072	0.02538
		Concentration^2	-	-	-	-	ns	0.74	0.000039	0.000037	ns	-	0.00044	0.00022431
LS		Concentration^3	-	-	-	-	-	-	-	-	ns	0.79	-8.91111E-7	4.930192E-7
		Intercept	-	-	31.14	0.26556	-	-	31.13	0.32610	-	-	31.19	0.34337
	S	Concentration	**	0.95	-0.021	0.00142	***	-	-0.021	0.00524	ns	-	-0.03	0.01317
		Concentration^2	-	-	-	-	ns	0.95	-1.66667E-7	0.00001673	ns	-	0.000085	0.00011644
		Concentration^3	-	-	-	-	-	-	-	-	ns	0.94	-1.88889E-7	2.559297E-7
		Intercept	-	-	13.26	0.30312	-	-	12.77	0.18640	-	-	12.81	0.18986
	R	Concentration	***	0.94	-0.02	0.00162	*	-	-0.008	0.003	ns	-	-0.02	0.00728
LA		Concentration^2	-	-	-	-	***	0.98	-0.00005	0.00001	ns	-	0.00002	0.00006
		Concentration^3	-	-	-	-	-	-	-	-	ns	0.98	-1.50556E-7	1.415141E-7
	S	Intercept	-	-	11.09	0.23398	-	-	10.82	0.22712	-	-	10.91	0.19318
		Concentration	***	0.96	-0.02	0.00125	*	-	-0.012	0.00365	**	-	-0.03	0.00741
		Concentration^2	-	-	-	-	*	0.97	-0.00003	0.000012	ns	-	0.00012	0.00007
		Concentration^3	-	-	-	-	-	-	-	-	ns	0.98	-3.25E-7	1.439897E-7
LR	R	Intercept	-	-	32.34	0.38425	-	-	32.60	0.442	-	-	32.61	0.48067
		Concentration	***	0.98	-0.05	0.00205	***	-	-0.06	0.007	*	-	-0.06	0.01844

Table 2: Contd.

	Concentration^2	-	-	-	-	-	0.98	0.00003	0.00002	ns	-	0.00004	0.00016
	Concentration^3	-	-	-	-	-	-	-	-	ns	0.98	-3.72222E-8	3.582687E-7
S	Intercept	-	-	29.06	0.55968	-	-	28.34	0.50744	-	-	28.37	0.55093
	Concentration	***	0.95	-0.04	0.00299	*	-	-0.02	0.0082	ns	-	-0.03	0.02114
	Concentration^2	-	-	-	-	*	0.97	-0.00007	0.00003	ns	-	-0.00004	0.0002
	Concentration^3	-	-	-	-	-	-	-	-	ns	0.96	-7.88889E-8	4.106416E-7

0.0005 x (Maroon) and Y = 0.25 - 0.0003 x (Darab)). This means that, although DWS response for these genotypes followed the same basic trend (linear model), the slope of predicted line differed for each genotype. R^2 values for Maroon and Darab were 0.93 and 0.94, respecttively. This means 93 and 94% of the variation was explained by the linear model. These values are high because R^2 values for biological data generally range from 0.50 to 0.90, whereas a low R^2 for non-biological data may be 0.90 (Kleinbaum and Kupper, 1978).

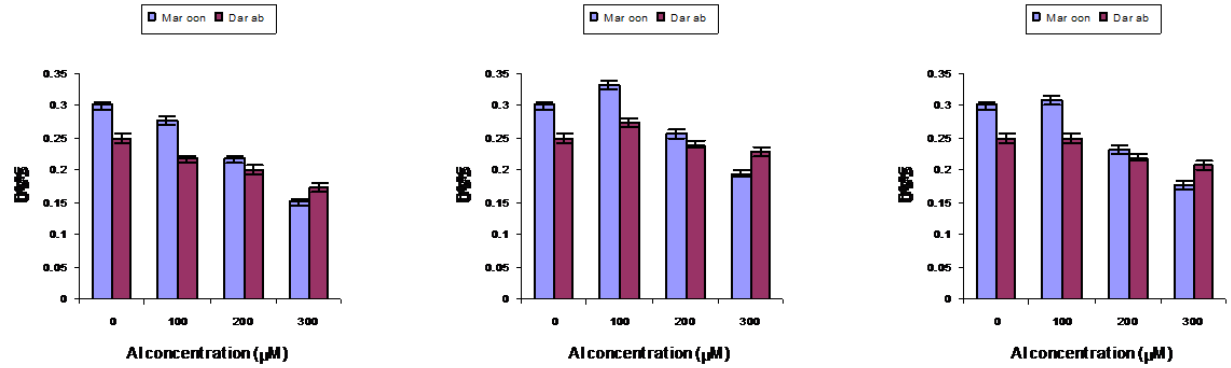
Analysis of DWR variable using polynomial contrasts indicated that, the response of Maroon and Darab explants also best fit the linear model and approximately had the same equations (Table 2). Concerning FWR trait, the response of Maroon best fit the quadratic model whereas Darab explants the linear model (Table 2). Analysis of FWS variable using polynomial contrasts indicated that, the response of Maroon and Darab explants best fit the linear and cubic models, respectively (Table 2). Response of Maroon and Darab LS best fit the linear model as indicated by a signi-significant T-value (Table 2) and approximately had the same equations. But R^2 values for Maroon and Darab were 0.74 and 0.95, respectively. This means that 74 and 95% of the variation was explained by the model. Analysis of LR variable using polynomial contrasts indicated that, the response of Maroon and Darab explants best fit the linear and quadratic model. R^2 values for Maroon and Darab were 0.98 and 0.97, respectively. This means that 98 and 97% of the variation was explained by the model. Response of Maroon and Darab LA best fit the quadratic model as indicated by a significant T-value (Table 2). R^2 values for Maroon and Darab were 0.98 and 0.97, respectively.

In the second experiment the effect of malate and citrate treatments was studied on reducing the noxious effect of Al in medium culture. ANOVA revealed that, there are significant differences among applied treatments on studied seedling growth parameters however, the interaction effects between applied treatment and Al concentration was significant in the studied traits (Table 3). This means that, the effect of malate or citrate application is effective in some Al concentrations compared to other Al concentrations. As shown in Figure 1, the application of malate especially in two first Al concentrations reduced the noxious effect of Al in medium culture in both studied genotypes. The results showed that, the application of malate were effective when compared with citrate treatment in reducing the noxious effect of Al (Figure 1).

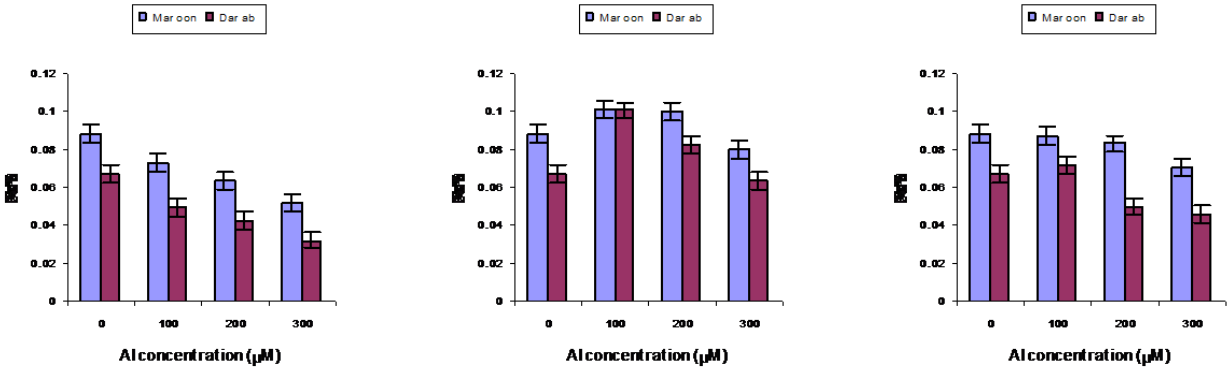
DISCUSSION

The results of the present study indicated that in Al-tolerant plants, Al caused less inhibition of root growth than that of Al-sensitive plants. One of the very early symptoms of aluminum toxicity is root growth inhibition, which can be accompanied by cell death as a consequence of the loss of plasma membrane (PM) integrity at higher aluminum concentrations (Matsumoto, 2000; Kochian, 1995). Several research works showed that, Al toxicity inhibits root cell division and elongation, thus reducing water and nutrient uptake, consequently resulting in poorer plant growth (Alam, 1981; Clarkson, 1966; Foy, 1983; Foy et al., 1967; Gauthier, 1953; Reid et al., 1969). Wallace et al. (1982) reported that wheat (*T. aestivum* L.) root elongation is affected within hours of Al exposure and as in many plant species; the primary site of Al toxicity in wheat appears to be the root apex (Bennet and Breen, 1991). Rayan and Kochian, (1993) have reported that root elongation in wheat and maize is inhibited only when apices are exposed to Al.

Our results showed that, in the both cultivars (Darab as Al sensitive and Maroon as aluminum tolerant) the application of malate and citrate as organic acids (Table 3) reduced the noxious effect of Al on seedling parameters. In some plants, the



LSD(0.05)=0.02



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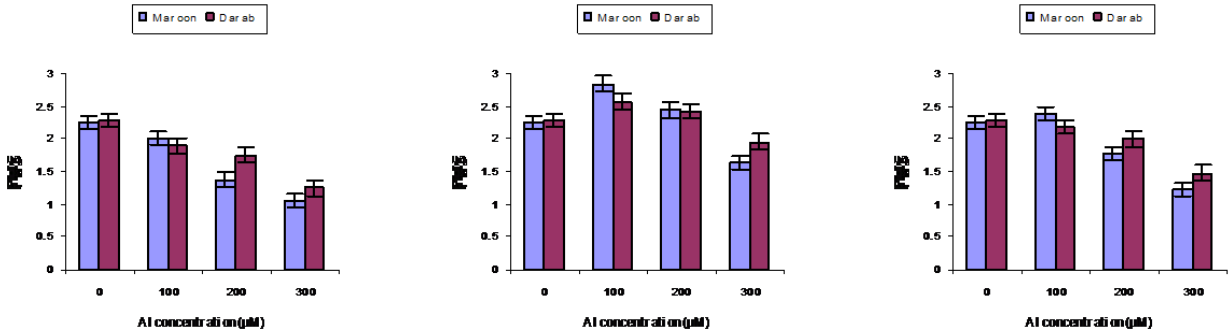
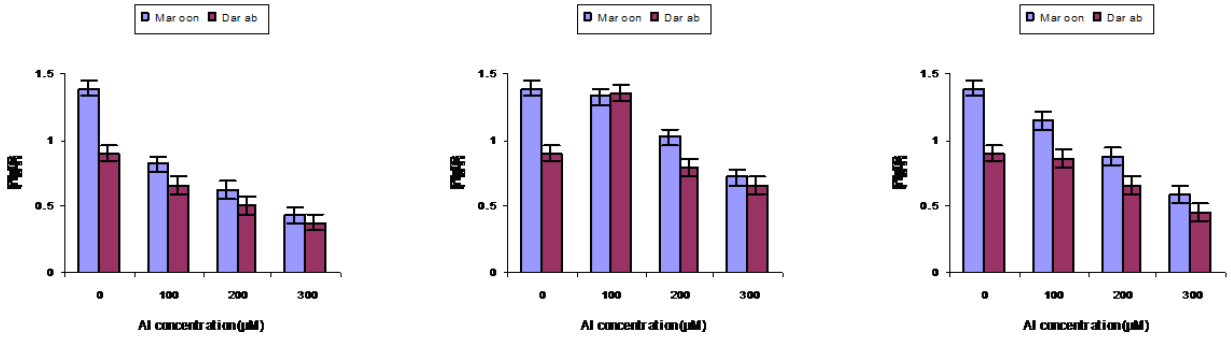
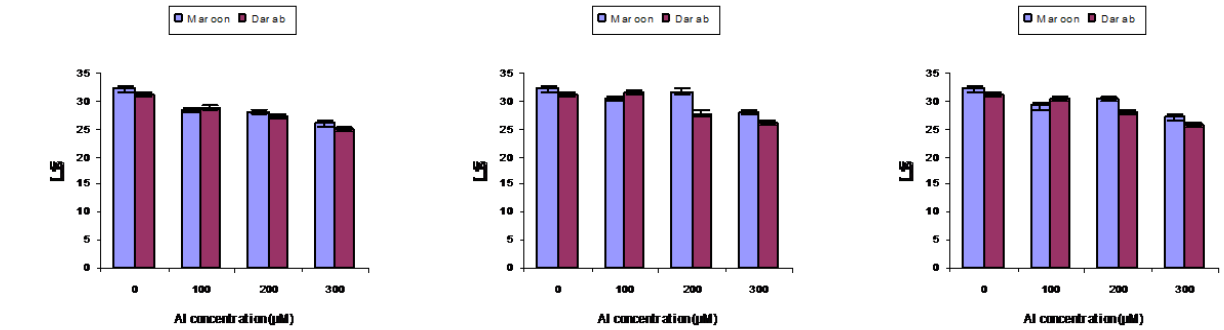


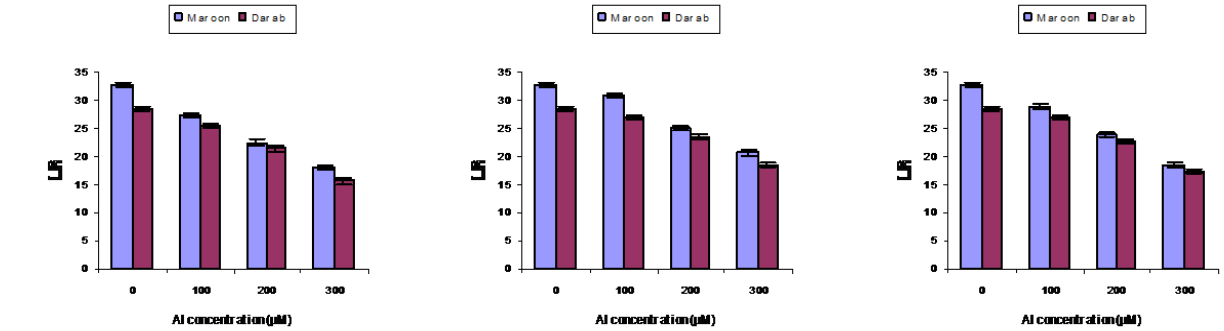
LSD(0.05)=0.33



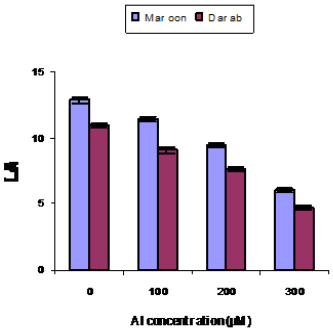
LSD(0.05)=0.17



LSD(0.05)=1.35



LSD(0.05)=1.16



LSD(0.05)=0.55

Figure1. Effect of malate and citrate treatments on reducing the noxious effect of Al in medium culture. The first column from left show the effect of only Al concentration in medium culture. The second column show the effect of Al concentration in medium culture together with the malate and the third column show the effect of Al concentration in medium culture together with the citrate on the different seedling parameters.

increased secretion of organic acids is localized in the root apex and depends upon the presence of Al in the external solution (Kollmeier and Horst, 2001; Ma et al., 2001; Zhang et al., 2001). The root apex is particularly sensitive to aluminum, therefore only the cations those immediately surrounding the apical root cells need to be detoxified. It has been shown that the organic acids, by forming chelates with Al, shield the root apex from the toxic Al cations by forming chelates with aluminum. Al resistance in wheat is correlated with the Al-activated efflux of malate from the root apices (Ryan et al., 1995) and this is consistent with our results observed as a correlation between malate application and Al resistance among the wheat lines.

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Table 3. Analysis of variance summary for wheat seedling growth parameters data under different Al concentrations including malate and citrate treatments. Data were analyzed using procedures for a completely randomized design.

Source	df	Mean of square						
		DWR	DWS	FWR	FWS	LS	LR	LA
Genotype	1	0.007**	0.01**	0.92**	0.09^{ns}	15.88**	112.63**	19.62**
Al concentration	3	0.002**	0.03**	1.35**	2.94**	90.45**	528.91**	45.96**
Treatment	2	0.004**	0.008**	0.56**	1.97**	13.67**	21.91**	0.28^{ns}
Genotype × treatment	2	0.0002^{ns}	0.00002^{ns}	0.02^{ns}	0.02^{ns}	0.92^{ns}	0.68^{ns}	-
Al concentration × treatment	6	0.0005**	0.001**	0.09**	0.23**	1.72*	2.58**	-
Genotype × Al concentration	3	0.00009^{ns}	0.007**	0.14**	0.18**	9.18**	7.33**	-
Genotype × Al concentration × treatment	6	0.00006^{ns}	0.00001^{ns}	0.01^{ns}	0.02^{ns}	0.93^{ns}	0.43^{ns}	-
Error	46	0.00006	0.0001	0.01	0.04	0.67	0.49	0.11
CV		11.16	4.53	12.63	9.45	2.81	2.82	3.68

CV, Coefficient of variation; df, degrees of freedom; ***, **, *, Significant at 0.001, 0.01 and 0.05 probability level; ns, non significant.

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