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INFLUENCE OF ALUMINUM ON MINERAL NUTRIENT UPTAKE AND ACCUMULATION IN *URTICA PILULIFERA* L.

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□ *Pollutants can have detrimental effects on living organisms. They can cause toxicity, damaging cells, tissues and organs because of their high concentrations or activities. Plants provide a useful system for screening and monitoring environmental pollutants. Among pollutants, aluminum is considered as a primary growth limiting factor for plants resulting in decreased plant growth and development. Although considered to be a non-essential and highly toxic metal ion for growth and development, aluminum (Al) is easily absorbed by plants.* Urticaceae *family members have high nutrient requirements demonstrated by leaves containing high levels of calcium (Ca), iron (Fe), magnesium (Mg), and nitrogen (N).* Urtica pilulifera *is one of the important traditional medicinal plants in Turkey. In this study,* U. pilulifera *was used as a bioindicator to investigate the possible differences in the absorption and accumulation of mineral nutrients at different levels of the Al exposure and examine the mineral nutrition composition of* U. pilulifera *under Al stress. Also, some growth parameters (leaf-stem fresh and dry weights, root dry weights, stem lengths and leaf surface area) were investigated.* U. pilulifera *seedlings were grown for two months in growth-room conditions and watered with spiked Hoagland solution, which contained 0, 100, and 200 μM aluminium chloride ($AlCl_3$). It was observed that macro- and micro-nutritional status of roots and leaves was altered by Al exposure. The concentrations of some macro- and micronutrients were reduced while concentrations of others were increased by excess of Al. Some macro- and micronutrients were increased at low level of Al whereas reductions were observed at high level of Al, and vice versa. The patterns were dependent on the macro- or micronutrient and the plant part.*

Keywords: mineral nutrient uptake, mineral nutrient accumulation, aluminum (Al) toxicity, Roman nettle, *Urtica pilulifera*

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INTRODUCTION

Aluminum (Al) is the most abundant metal in the earth's crust and one of the most important components of the soil (7%). Also it is soluble as a trivalent ionic form is highly active in acid soil (pH < 5.0) and is considered as a primary growth limiting factor for plants resulting in decrease plant growth and development (Thornton et al., 1986; Kochian, 1995; Matsumoto, 2000). Among the common effects of Al are: decrease in total leaf number and size, a decrease in shoot biomass, inhibition of root elongation, and chlorosis and necrosis of leaves, leading to decreased photosynthetic activity (Thornton et al., 1986; Kochian, 1995; Jones and Kochian, 1995). Aluminum also causes ultrastructural and cellular changes in leaves, as cell division and elongation are inhibited, and reduces stomatal aperture (Rengel, 1992; Kochian, 1995; Delhaize and Ryan, 1995).

Aluminum does not exert any known function in plant metabolism (Foy, 1984; MacDonald and Martin, 1988). Among the ongoing research focused on Al toxicity are those affecting a large number of cellular processes. Al can inhibit the uptake of potassium (K^+) (Liu and Luan, 2001), calcium (Ca^{2+}) (Huang et al., 1992), and magnesium (Mg^{2+}) (Keltjens, 1995), and interacts with both microtubules and actin filaments leading to deleterious effects on cytoskeletal dynamics (Blancaflor et al., 1998; Sivaguru et al., 1999, 2000; Silva et al., 2000). Aluminum modifies composition, physical properties, and structure of the cell wall and plasma membrane (Wagatsuma et al., 1995; Zhang et al., 1997; Ishikawa and Wagatsuma, 1998) and affects phosphate and/or nucleotide metabolism (Matsumoto and Morimura, 1980; Wallace and Anderson, 1984). Aluminum interference with the signal transduction pathway could also play a role in Al toxicity (Jones and Kochian, 1995; Jones et al., 1998; Ramos-Diaz et al., 2007). Al may cause oxidative stress, which could be involved in Al inhibition of root growth (Yamamoto et al., 2002). It also induces the secretion of organic acids from roots (Delhaize and Ryan, 1995; Ma et al., 2001) and long term exposure to Al and inhibition of root growth generally leads to nutrient deficiencies mainly of Ca, Mg, and phosphorus (P) by interfering with the uptake, transport, and utilization of nutrients (Kidd and Proctor, 2000; Scholl et al., 2005). Al induces deficiency of nutrients by adversely affecting the root system causing inhibition of root elongation and restricting absorption of mineral elements and water (Slaski, 1994) leading to mineral deficiencies in shoots and leaves (Foy, 1988). Although regarded as a toxic element, Al frequently stimulates growth at low concentrations (Foy, 1984; Kinraide, 1993).

Urticaceae family members are very common and widespread species found in the margins of arable fields, gardens and countryside throughout Europe, Asia, and Northern Africa (Firbank et al., 2002). Members of this family have high nutrient requirements demonstrated by leaves containing high levels of Ca, Mg, nitrogen (N) (Grime et al., 1988; Wilman and Riley,

1993) and iron (Fe) (Salisbury, 1962). *Urticaceae* family member species have been used as medicinal plants for years all over the world (Kavalali et al., 2003) and leaves of *Urtica* are nutritious and rich in micronutrients (Emmelin and Feldberg, 1949; Wagner et al., 1994). *Urtica pilulifera* (Roman nettle) is one of the most important traditional drugs in Turkey (Baser et al., 1986). The whole plant shows antiasthmatic, antidandruff, astringent, depurative, diuretic, expectorant, purgative, galactogogue, haemostatic, and hypoglycemic effects, and is a stimulatory tonic used for medicinal purposes. It was especially used as a remedy for diabetes mellitus, eczema, rheumatism, hemorrhoids, hyperthyroidism, bronchitis, and cancer (Baytop, 1999; Kavalali et al., 2003).

Higher plants provide a useful system for screening and monitoring environmental pollutants (Grant, 1994; Yasar et al., 2010). In this study, *U. pilulifera* was used as a bioindicator to investigate the effects of different levels of the Al exposure and examine the difference on mineral nutrition uptake and accumulation of *U. pilulifera*.

MATERIALS AND METHODS

Growing Seeds

The *U. pilulifera* seeds were surface-sterilized by immersion in ethyl alcohol (50%) for 1 minute followed by deionized water for 5 minutes. They were then transferred into small vessels containing sterilized compost for germination. During the germination period (2 weeks), the seeds were moistened with deionized water. When the shoot lengths of the young plantlets reached 3–4 cm, they were transferred into standard plastic pots containing sterilized compost and maintained under growth-room conditions. The plants were grown under fluorescent tubes give an irradiance in 5000 μmol m^{-2} s^{-1}. (day/night-16/8 respectively), and a temperature of 23 $\pm$ 2°C and relative humidity 45–50%. Each of the experimental groups of eight replicates was watered with Hoagland nutrient solution (Hoagland and Arnon, 1950) at two-day intervals for the 2 months during which the stress treatments were applied.

Application of Al

While control plants were watered only with Hoagland solutions, the experimental groups were watered with spiked Hoagland solutions [prepared as 100 and 200 μM aluminum chloride ($AlCl_3$)]. Each treatment was watered with 40 ml of solution at two-day intervals. The soil pH was adjusted to 4 for Al treatments using 0.2% (v/v) sulfuric acid (H_2SO_4).

Analytic Techniques

Seedlings were harvested at the end of the two-month experiment period. Some growth parameters such as stem length, fresh and dry weight of leaves and stems, and leaf area, were measured at the end of the study. However, root fresh weights were not measured because of some problems in removing soil particles on the fresh roots. Plant leaves and roots were isolated and oven-dried at 80°C for 24 h, milled in micro-hammer cutter and fed through a 1.5-mm sieve. Samples were weighed as 0.5 g and transferred into Teflon vessels and then 8 ml of 65% (v/v) nitric acid (HNO_3) (Merck, Darmstadt, Germany) was added. Samples were mineralized in a Berghof MWS-2 microwave oven (Berghof, Eningen, Germany) as follows: in 145°C for 5 min, in 165°C for 5 min and in 175°C for 20 min. After cooling, the samples were filtered by Whatman filters (GE Healthcare, Fairfield, CT, USA), and made up to 50 ml with ultra pure water in volumetric flasks and then stored in sterile falcon tubes. Standard solutions were prepared by using multi element stock solutions-1000 mg kg^{-1} DW and mineral element [Al, Ca, Fe, K, Mg, manganese (Mn), sodium (Na), P, sulfur (S) and zinc (Zn)] measurements were done by Inductively Coupled Plasma Optical Emission Spectroscopy (ICP-OES) (PerkinElmer-Optima 7000 DV, PerkinElmer, Grayson, GA, USA).

Statistical Calculations

The standard error values of the means were calculated to compare the site categories. Statistical analysis was performed using a one way analysis of variance (ANOVA) (for $P < 0.05$). Based on the ANOVA results, a Tukey test for mean comparison was performed, for a 95% confidence level to test for significant differences among treatments.

RESULTS AND DISCUSSION

The growth and uptake and accumulation of macro- and micronutrients are altered extensively in plants grown with Al. Interactions of Al with other macro- and micronutrients have been suggested as factors affecting inhibitory effects of Al (Foy, 1974). It is generally known that plants grown with Al at low pH exhibit a variety of nutrient-deficiency symptoms, with a consequent decrease in biomass. In the present study, the effect of increasing Al ion activity on shoot, stem, and root growth is shown in the Table 1. There is a reduction in both leaf and root fresh and dry weights, with increasing reduction observed at higher levels of Al (Table 1). There is an increase in stem fresh weight at low concentration of Al and then following a slight decrease at high concentration of Al, but stem dry weights increased at both concentrations of Al, with increasing stem biomass observed at higher

TABLE 1 Some growth parameters of *U. Pilulifera* in different Al levels (0, 100, and 200 μM) in two months of growing period. All units of measure are per pot. According to the results of variance analysis and Tukey's test, the mean difference is significant at 0.05 levels

	Control	Al 100 μM	Al 200 μM
Stem length (cm)	25.58 ± 0.88*	33.68 ± 0.8*	37.52 ± 0.64*
Leaf fresh weight (g)	4.78 ± 0.14*	4.06 ± 0.19*	3.46 ± 0.31*
Leaf dry weight (g)	1.04 ± 0.03*	0.98 ± 0.04	0.88 ± 0.03*
Stem fresh weight (g)	3.66 ± 0.16*	4.65 ± 0.2	4.6 ± 0.46
Stem dry weight (g)	1.33 ± 0.08*	1.43 ± 0.07*	1.51 ± 0.14
Root dry weight (g)	1.94 ± 0.07*	1.92 ± 0.12	1.68 ± 0.18
Leaf area (cm^2)	39.26 ± 0.42*	51.15 ± 1.3*	55.05 ± 1.51*

Variance analysis and Tukey test are indicated ($P < 0.05$ significant).

levels of Al (Table 1). At the same time, enhancement of stem lengths and leaf areas at both low and high concentrations of Al have been observed but the degree of enhancements have been slowed at high concentration of Al when compared with low concentration of Al (Table 1). Al toxicity is an important growth-limiting factor for plants. Al interferes with a wide range of physical and cellular processes. Potentially, Al toxicity could result from complex Al interactions with apoplastic, plasma membrane, and symplastic targets. Aluminum ions are taken up by plants through the root system and are predominantly accumulated in the epidermis and in the outer cortex (Wagatsuma et al., 1987; Delhaize et al., 1993). The endodermis possibly acts as a barrier, and transport to the shoot and leaves is generally small. This is consistent with the results of the present study. The data shows that much of Al ions are held by the root system and only a small fraction is transferred from root to shoot. At first, exposure to Al causes stunting of the primary root and inhibition of lateral root formation. Affected roots are stubby and inefficient in absorbing both nutrients and water (Rengel, 1992) due to inhibition of cell elongation and cell division (Ryan et al., 1993; Kochian, 1995), disruption of calcium and potassium utilization (Jones et al., 1998; Plieth et al., 1999), decrease root respiration (Yamamoto et al., 2001), callose deposition in plasma membrane and plasmodesmata (Sivaguru et al., 2000), and the deposition of polysaccharides in cell walls by increasing synthesis of hemicellulose, cellulose, and pectin. These carbohydrates may help to trap Al in the apoplast, but may further disrupt cell elongation (Tabuchi and Matsumoto, 2001; Teraoka et al., 2002). Damaged root systems can explore only a limited volume of soil and are incapable of absorbing nutrients and water (Wright, 1989). Water deficiency causes the closure of stomata (Epstein and Grant, 1973; Quick et al., 1992), which decreases both transpiration and photosynthesis in many plants (Zelitch, 1971; Fatemy et al., 1985). It also affects many other metabolic pathways, mineral uptake, membrane structure, stomatal structural changes and conductance, and carbon dioxide (CO_2) uptake (Davies and Zhang, 1991; Tardieu and Davies, 1993; Davies, 1995).

The common responses of root and shoot to Al are a decrease in root and shoot biomass, with increasing decrease observed at higher levels of Al. This is also observed in the present study. Stem length and biomass increased as compared to the control (Table 1). An increase in area of leaves was also observed in 60-day Al treated (100 and 200 μM) *U. pilulifera* although there was a decrease in leaf fresh and dry weights (Table 1). Plant cells respond to stress factors in different ways depending on their tissue type. In the present study, although there was an increase in the leaf area, structural cell degeneration was observed at palisade and spongy parenchyma after Al exposure. This cell degeneration was severe at both 100 and 200 μM $AlCl_3$. As a result of this, reduced lamina thickness was observed. In conjunction, reduced lamina thickness explains the reduced leaf biomass. Decreased chlorophyll was monitored as an indicator of Al toxicity (Zhang et al., 2008). According to Barnabas et al., 2000, Al affects photosynthesis by lowering the chlorophyll content and reducing electron flow. In addition, Al-stress-induced loss in chlorophyll has been reported in many plant species like wheat, lemma, sage, sorghum, rice, lentil, potato, and tobacco (Ohki, 1986; Gardner and Al-Hamdani, 1997; Severi, 1997; Kuo and Kao, 2003; Tabaldi et al., 2007; Zhang et al., 2008; Azmat and Hasan, 2008). Decline in chlorophyll (Chl) a/b ratio was observed in *Oryza sativa* grown in the presence of excess Al (Sarkunan et al., 1984). Both concentrations of Al (100 and 200 μM) caused significant increase in leaf area whereas stem biomass was also increased. The results revealed that the anatomical changes in leaf and stem were because of inefficient nutrient and water uptake and consequently reduced photosynthetic activity. It is believed that *U. pilulifera* tried to compensate the reduced photosynthetic activity by increasing the leaf area and strengthening the stem. Overall, although symptoms of Al toxicity are also manifested in the shoots, these are usually regarded as a consequence of injuries to the root system.

Table 2 shows Al concentrations in roots and leaves of *U. pilulifera* grown in different Al levels. Aluminum concentration in *U. pilulifera* increased dramatically with Al levels. There was a large difference in Al concentrations among the roots and leaves of *U. pilulifera*. The concentration of Al was increased significantly in roots and did not differ at 100 μM Al treatments but increased at 200 μM Al treatments in leaves by the presence of Al (Table 2). The differences between the roots and leaves of *U. pilulifera* were very high for 100 μM and 200 μM Al treatments. For example, Al concentration in roots of 100 μM and 200 μM Al treatments were about 1643 and 731 fold higher, respectively, than that in leaves. The data shows that Al itself mainly accumulated in the roots and only small amounts of Al were transported into the leaves.

In *U. pilulifera* seedlings grown under different Al levels, the concentrations of some macro- and micronutrients were examined in leaves and roots at 60-day of Al exposure. It is clear from the results that macro- and micronutrient composition in roots and shoots was altered by Al exposure. The

TABLE 2 Concentrations of Ca, Fe, K, Mg, Mn, Na, P, S, and Zn (mg kg^{-1} dw) in leaf and root samples of *U. pilulifera* grown in different Al (0, 100, and 200 μM) levels for two months. According to the results of variance analysis and tukey test, the mean difference is significant at 0.05 levels

		Control	Al 100 μM	Al 200 μM
Al (mg kg^{-1})	Leaf	0.00 ± 0.00	0.00 ± 0.00	11.31 ± 0.22*
	Root	0.00 ± 0.00	1643.3 ± 45.1*	8276.67 ± 64.7*
Ca (mg kg^{-1})	Leaf	12415.0 ± 104.6*	8171.25 ± 99.15*	5258.0 ± 25.3*
	Root	2491.3 ± 94.8*	4769.67 ± 50.78*	5201.67 ± 28.07*
Fe (mg kg^{-1})	Leaf	123.59 ± 3.98*	99.03 ± 0.97*	124.98 ± 1.05*
	Root	1610.0 ± 38.41*	2028.63 ± 34.28*	1204.67 ± 59.44*
K (mg kg^{-1})	Leaf	15222.25 ± 149.24*	11830.0 ± 116.06*	8478.25 ± 110.1*
	Root	4365.0 ± 73.04*	3194.0 ± 34.7*	2589.3 ± 35.4*
Mg (mg kg^{-1})	Leaf	5436.25 ± 176.64*	6384.5 ± 135.09*	4564.75 ± 13.4*
	Root	2159.3 ± 11.53*	1998.67 ± 53.34*	2313.0 ± 80.23*
Mn (mg kg^{-1})	Leaf	20.25 ± 0.71*	53.27 ± 0.87*	81.84 ± 1.24*
	Root	21.58 ± 0.38*	68.11 ± 0.31*	84.48 ± 0.92*
Na (mg kg^{-1})	Leaf	922.88 ± 15.2*	2356.8 ± 38.24*	1992.5 ± 35.57*
	Root	2519.3 ± 21.15*	1914.0 ± 7.69*	1596.0 ± 25.33*
P (mg kg^{-1})	Leaf	3253.25 ± 36.8	3435.0 ± 15.34*	3177.0 ± 52.28
	Root	2917.0 ± 82.29	4313.0 ± 20.74	3540.67 ± 16.02*
S (mg kg^{-1})	Leaf	9313.5 ± 110.25	10434.0 ± 282.8	9087.0 ± 43.65*
	Root	4611.67 ± 185.7	7860.67 ± 143.9	10246.67 ± 32.35*
Zn (mg kg^{-1})	Leaf	28.42 ± 0.36*	35.5 ± 0.93*	23.01 ± 0.49*
	Root	26.4 ± 0.9*	32.85 ± 0.52*	66.6 ± 1.78*

Variance analysis and Tukey test are indicated ($P < 0.05$ significant).

macro- and micronutrient concentrations in *U. pilulifera* plant tissues are shown in Table 2. There existed significant differences in the accumulation of some macro- and micronutrients in both roots and leaves of *U. pilulifera* seedlings under Al stress. The concentrations of several macro- and micronutrients were reduced by the presence of Al. Root concentration of K and Na and leaf concentration K and Ca was reduced by the Al treatment, with the greatest reduction observed at higher levels of Al (Table 2). Contents of Ca, Mn, S, and Zn in roots and Mn and Na in leaves were increased in the presence of Al, with the greatest increase observed at higher levels of Al (Table 2). For root concentration of P and Fe and leaf concentration of Zn and Mg, a slight increase at 100 μM Al was found relative to the control, and showed marked decrease with increasing Al level (100 μM-200 μM) (Table 2). No significant difference in root concentration of Mg and in leaf concentration of P, S, and Fe were found between any Al treatment and the control (Table 2).

In our study, concentration of K in leaves and roots was reduced at both levels of Al. It was demonstrated that Al may block channels conducting influx of K^+ in guard cells (Schroeder, 1988) and also corresponding channels in wheat roots (Gassmann and Schroeder, 1994) and by blocking K^+ channel, turgor-driven cell elongation would be interfered (Liu and Luan, 2001). Aluminum may enhance transport of K^+ from cells by channels in plants (Hedrich and Neher, 1987; Tester, 1990). Aluminum stimulates the efflux of both malate and K^+ from root apices of other wheat cultivars (Delhaize et al., 1993; Ryan et al., 1995). By binding of Al to the root membrane, an increase in K^+ efflux is possible (Wagatsuma et al., 1987). Given information shows consistency with the present results.

Concentration of Ca was increased in roots but decreased in leaves at both levels of Al in *U. pilulifera* seedlings. An Al-induced increase in Ca was found in root protoplasts of wheat (Lindberg and Strid, 1997). Al can also decrease the cytosolic level of Ca^{2+} by acting as a Ca-channel blocker in the plasma membrane (Pineros and Tester, 1995). This is consistent with the present results. An increase in the cytosol Ca^{2+} depended on inhibition of the Ca^{2+}-channels by Al or on stimulated transport of Ca^{2+} through channels was dependent on the specific plant parts.

In our investigation, P and S uptake were increased in root cells at both levels of Al comparing with the control, but for P the degree of increment was lower at 200 μM Al. Al can form complexes with P and S at any pH (Foy et al., 1978). Because of the precipitation of P and S with Al as Al phosphate and Al sulfate may result in high P and S contents in roots (McCormick and Borden, 1972). Similar values were obtained in the present experiment. Following this, P and S deficiencies were expected in leaves but a slight increase at low level of Al and then following the increment, a slight decrease at high level of Al were observed in leaves comparing with the control for both P and S. Concentrations of P and S in the leaves of *U. pilulifera* were not affected significantly by any of Al treatments. The high nutrient concentrations in soil might enable sufficient nutrient uptake by plants, even when root vitality and nutrient uptake capacity are reduced by Al (Foy et al., 1978).

Al treatments increased the concentration of Mn and Zn in roots and leaves at both levels of Al, with increasing increments at high levels of Al. For Zn at high level of Al treatment, a decrease was observed following the increment at low level of Al treatment in leaves. Regarding the acquisition of relatively unavailable micronutrients such as Zn and Mn from the soil, terrestrial plants have evolved sophisticated strategies. These essential macro- and micronutrients at the same time are potentially very toxic to plants. Due to this potential toxicity, the uptake, transport, and accumulation of these macro- and micronutrients is highly coordinated and regulated by plants (Kochian et al., 2002). The transmembrane proton (H^+) gradient serves as the major driving force for secondary ion transport processes. H^+-ATPase is responsible for the formation and maintenance of the transmembrane H^+ gradient. Al-induced inhibition of H^+-ATPase activity and as consequent of disruption of the H^+ gradient could indirectly alter ionic status and ion homeostatis of root cells (Kochian et al., 2005). Changes in ionic strength, pH, the concentration of other elements and complexing ligands can have effects on the activity of cells. As a consequence of these events, a number of stress responses can be produced such as expression of oxidative stress genes (Ezaki et al., 2000; Milla et al., 2002) and making the synthesis of several proteins (Basu et al., 1994). For example, increased expression, resulting from changes in the plant Zn and Mn status could lead to increased Zn and Mn influx in the roots and shoots. Plants accumulate sufficient Na^+ salts in vacuoles to maintain turgor and growth if water potentials are low (Hellebust, 1976; Jennings, 1976). Aluminum interrupts water uptake (Rengel, 1992). Data shows that there was an increase in leaves at both levels of Al treatments although the increment was slowed at high level of Al treatment. Similarly, in the present study, Na^+ might have been accumulated in vacuoles of leaves to maintain turgor because of water stress. Experimental data showed that Fe concentrations in roots and leaves were influenced by Al treatments. In roots, there was an increase at low level of Al and then a decrease at high level of Al. On contrary, there was a reduction at 100 μM Al and following the reduction, an increase was observed at 200 μM Al. Those increments and reductions were small in both roots and leaves. There was antagonism between Fe and Zn in leaves. Fe concentration was reduced with increasing Zn concentration at low level of Al treatment but at high level of Al treatment, Fe concentration was increased while Zn concentration was reduced. Zn-induced inhibition of Fe translocation from roots to leaves was observed. It was observed that increased Zn greatly increased translocation of Mn to soybean tops (White et al., 1974). A similar result was obtained in the present study. It seems that there are complex interactions between major ions including essentials and nonessentials for plants.

Al can interrupt the uptake of many cations including Ca^{2+}, Mg^{2+}, K^+, and NH_4^+ (Huang et al., 1992; Rengel and Elliott, 1992; Nichol et al., 1993; Ryan and Kochian, 1993). The root-cell ion transport proteins can be blocked directly by Al. For example, recently some evidence has been presented that Al^{3+} interacts directly with several different plasma membrane channel proteins, blocking the uptake of ions such as K^+ and Ca^{2+} (Gassmann and Schroeder, 1994; Pineros and Tester, 1995; Pineros and Kochian, 2001). Because of ionic size similarities between Mg^{2+} and Al^{3+}, displacement of Mg^{2+} by Al^{3+} in biological systems is possible. The negative effect of Al on concentration of Mg^{2+} may be explained by ion antagonism at uptake sites although there was a slight decrease at low level of Al and an increase following the reduction at high level of Al in roots and vice versa in leaves. The initial increment at low level of Al in leaves could be the result of alleviation of H^+ toxicity. Similarly, Andrew et al. (1973) reported that Al treatment had little effect on Mg levels.

In conclusion, it was observed that some growth parameters (leaf-stem fresh and dry weights, root dry weights, stem lengths, and leaf surface area) of *U. pilulifera* were extensively altered by Al exposure and Al interferes with the uptake, transport, and use of several macro- and micronutrients. Excess of Al reduces the uptake of certain elements and increases that of others, the patterns being dependent on the element and the plant part involved.

REFERENCES

Andrew, C. S., A. D. Johnson, and R. L. Sandland. 1973. Effect of aluminium on the growth and chemical composition of some tropical and temperate pasture legumes. *Australian Journal of Agricultural Research* 24: 325–339.

Azmat, R., and S. Hasan. 2008. Photochemistry of light harvesting pigments and some biochemical changes under aluminium stress. *Pakistan Journal of Botany* 40: 779–784.

Barnabas, B., G. Kovacs, A. Hegedus, L. S. Erdei, and G. Horvath. 2000. Regeneration of doubled haploid plants from in vitro selected microspores to improve aluminum tolerance in wheat. *Journal of Plant Physiology* 156: 217–222.

Baser, K. H. C., G. Honda, and W. Miki. 1986. *Herbs, Drugs and Herbalists in Turkey*. Tokyo, Toyo Publishing.

Basu, U., D. Godbold, and G. J. Tayor. 1994. Aluminum resistance in *Triticum aestivum* associated with enhanced exudation of malate. *Plant Physiology* 144: 747–753.

Baytop, T. 1999. *Treapy with Medicinal Plants in Turkey (Past and Present)*. Istanbul: Istanbul University.

Blancaflor, E. B., D. L. Jones, and S. Gilroy. 1998. Alterations in the cytoskeleton accompany aluminum-induced growth inhibition and morphological changes in primary roots of maize. *Plant Physiology* 118: 159–172.

Davies, P. J. 1995. The plant hormone concept: concentration, sensitivity and transport. In: *Plant Hormones*, eds. P. J. Davies, pp. 13–38. Dordrecht, the Netherlands: Kluwer Academic Publishers.

Davies, W. J., and J. Zhang. 1991. Root signals and the regulation of growth and development of plants in drying soil. *Annual Review of Plant Physiology and Plant Molecular Biology* 42: 55–76.

Delhaize, E., and P. R. Ryan. 1995. Aluminum toxicity and tolerance in plants. *Plant Physiology* 107: 315–321.

Delhaize, E., P. R. Ryan, and P. J. Randall. 1993. Aluminum tolerance in wheat (*Triticum aestivum* L.): II. Aluminum stimulated excretion of malic acid from root apices. *Plant Physiology* 103: 695–702.

Emmelin, N., and W. Feldberg. 1949. Distribution of acetycholine and histamine in nettle plants. *New Phytologist* 48: 143–148.

Epstein, E., and W.J. Grant. 1973. Water stress relations of the potato Bull. 843. Plant under field conditions. *Agronomy Journal* 65: 400–404.

Ezaki, B., R. C. Gardner, Y. Ezaki, and H. Matsumoto. 2000. Expression of aluminum-induced genes in transgenic *Arabidopsis* plants can ameliorate aluminum stress and/or oxidative stress. *Plant Physiology* 122: 657–665.

Fatemy, F., P. K. E. Trinder, J. N. Winngfiel, and K. Evans. 1985. Effects of *Globodera rostochiensis*, water stress and exogenous abscisic acid on stomotal function and water use of Cara and Pentland Dell potato plants. *Revue Nematology* 8: 249–255.

Firbank, L. G., L. R. Norton, and S. M. Smart. 2002. Recording Cereal Field Margins in Countryside Survey 2000. Report to the Department for Environment, Food and Rural Affairs, 16. Centre for Ecology and Hydrology (Natural Environment Research Council), MAFF contract BD1902, CEH Project C00759.

Foy, C. D. 1974. Effects of aluminum on plant growth. In: *The Plant Root and its Environment*. ed. E. W. Carson, pp. 601–642. Charlottesville, VA: University of Virginia Press.

Foy, C. D. 1984. Physiological effects of hydrogen, aluminum, and manganese toxicities in acid soil. In: *Soil Acidity and Liming*, ed. F. Adams, pp. 57–97. Madison, WI: American Society of Agronomy.

Foy, C. D. 1988. Plant adaptation to acid, aluminum-toxic soils. *Communications in Soil Science and Plant Analysis* 19: 959–987.

Foy, C. D., R. L. Chaney, and M. C. White. 1978. The physiology of metal toxicity in plants. *Annual Review of Plant Physiology* 29: 511–566.

Gardner, J. L., and S. H. Al-Hamdani. 1997. Interactive effects of aluminum and humic substances on salvinia. *Journal of Aquatic Plant Management* 35: 30–34.

Gassmann, W., and J. I. Schroeder. 1994. Inward-rectifying K^+ channels in root hairs of wheat: A mechanism for aluminium-sensitive low-affinity K^+ uptake and membrane potential control. *Plant Physiology* 105: 1399–1408.

Grant, W. F. 1994. The present status of higher plant bioassay for the detection of environmental mutagens. *Mutation Research* 310: 175–185.

Grime, J. P., J. G. Hodgson, and R. Hunt. 1988. *Comparative Plant Ecology*. London: Unwin Hyman Ltd.

Hedrich, R., and E. Neher. 1987. Cytoplasmic calcium regulates voltage-dependent ion channels in plant vacuoles. *Nature* 329: 833–835.

Hellebust, J. A. 1976. Osmoregulation. *Annual Review of Plant Physiology* 27: 485–505.

Hoagland, D. R., and D. I. Arnon. 1950. The water culture method for growing plants without soil. Circular 347. Berkeley, CA: Agricultural Experimental Station, University of California.

Huang, J. W., D. L. Grunes, and L. V. Kochian. 1992. Aluminum effects on the kinetics of calcium uptake into cells of the wheat root apex. *Planta* 188: 414–421.

Ishikawa, S., and T. Wagatsuma. 1998. Plasma membrane permeability of root-tip cells following temporary exposure to Al ions is a rapid measure of Al tolerance among plant species. *Plant and Cell Physiology* 39: 516–525.

Jennings, D. H. 1976. The effect of sodium chloride on higher plants. *Biological Reviews* 51: 454–486.

Jones, D. L., and L. V. Kochian. 1995. Aluminum inhibition of the inositol 1–4–5-triphosphate signal transduction pathway in wheat roots: A role in aluminum toxicity? *The Plant Cell* 7: 1913 –1922.

Jones, D. L., L. V. Kochian, and S. Gilroy. 1998. Aluminum induces a decrease in cytosolic calcium concentration in BY-2 tobacco cell cultures. *Plant Physiology* 116: 81–89.

Kavalali, G., H. Tuncel, S. Goksel, and H. H. Hatemi. 2003. Hypoglycemic activity of *Urtica pilulifera* in streptozotocin-diabetic rats. *Journal of Ethnopharmacology* 84: 241–245.

Keltjens, W. G. 1995. Magnesium uptake by Al-stressed maize plants with special emphasis on cation interactions at root exchange sites. *Plant and Soil* 171: 141–146.

Kidd, P. S., and J. Proctor. 2000. Effect of aluminum on the growth and mineral composition of *Betula pendula* Roth. *Journal of Experimental Botany* 51: 1057–1066.

Kinraide, T. B. 1993. Aluminum enhancement of plant growth in acid rooting media- a case of reciprocal alleviation of toxicity by two toxic cations. *Physiologia Plantarum* 88: 619–625.

Kochian, L. V. 1995. Cellular mechanisms of aluminium toxicity and resistance in plants. *Annual Review of Plant Physiology and Plant Molecular Biology* 46: 237–260.

Kochian, L. V., N. S. Pence, L. D. Letham, M. A. Pineros, J. V. Magalhaes, O. A. Hoekenga, and D. F. Garvin. 2002. Mechanisms of metal resistance in plants: aluminum and heavy metals. *Plant and Soil* 247: 109–119.

Kochian, L. V., M. A. Pineros, and O. A. Hoekenga. 2005. Tle physiology, genetics and molecular biology of plant aluminum resistance and toxicity. *Plant and Soil* 274: 175–195.

Kuo, M. C., and C. H. Kao. 2003. Aluminum effects on lipid peroxidation and antioxidative enzyme activities in rice leaves. *Biologia Plantarum* 46: 149–152.

Lindberg, S., and H. Strid. 1997. Aluminium induces rapid changes in cytosolic pH and free calcium and potassium concentrations in root protoplasts of wheat (*Triticum aestivum*). *Physiologia Plantarum* 99: 405–414.

Liu, K., and S. Luan. 2001. Internal aluminum block of plant inward K^+ channels. *The Plant Cell* 13: 1453–1465.

Ma, J. F., P. R. Ryan, and E. Delhaize. 2001. Aluminium tolerance in plants and the complexing role of organic acids. *Trends in Plant Science* 6: 273–278.

MacDonald, T., and R. B. Martin. 1988. Al ion in biological systems. *Trends in Biological Science* 13: 15–19.

Matsumoto, H. 2000. Cell biology of aluminum toxicity and tolerance in higher plants. *International Review of Cytology* 200: 1–46.

Matsumoto, H., and S. Morimura. 1980. Repressed template activity of chromatin of pea roots treated by aluminum. *Plant and Cell Physiology* 21: 951–959.

McCormick, L. H., and F. Y. Borden. 1972. Phosphate fixation by aluminum in plant roots. *Soil Science Society of America Proceedings* 36: 799–802.

Milla, M. A .R., E. Butler, A. R. Huete, C. F. Wilson, O. Anderson, and J. P. Gustafson. 2002. Expressed sequence tag-based gene expression analysis under aluminum stress in rye. *Plant Physiology* 130: 1706–1716.

Nichol, B. E., L. A. Oliveria, A. D. M. Glass, and M. Y. Siddiqi. 1993. The effects of aluminum on the influx of calcium, potassium, ammonium, nitrate, and phosphate in an aluminum–sensitive cultivar of barley (*Hordeum vulgare* L.). *Plant Physiology* 101: 1263–1266.

Ohki, K. 1986. Photosynthesis, chlorophyll and transpiration responses in aluminum stressed wheat and sorghum. *Crop Science* 26: 572–575.

Plieth, C., B. Sattelmacher, U. P. Hansen, and M. R. Knight. 1999. Low-pH-mediated elevations in cytosolic calcium are inhibited by aluminum: A potential mechanism for aluminum toxicity. *The Plant Journal* 18: 643–650.

Pineros, M., and L. V. Kochian. 2001. A patch clamp study on the physiology of aluminum toxicity and aluminum tolerance in *Zea mays*: identification and characterization of Al^{3+} -induced anion channels. *Plant Physiology* 125: 292–305.

Pineros, M., and M. Tester. 1995. Characterization of a voltage-dependent Ca^{2+} –selective channel from wheat roots. *Planta* 195: 478–488.

Quick, W. P., M. M. Chaves, R. Wendler, M. David, M. L. Rodrigues, J. A. Passaharinho, J. S. Pereira, M. D. Adcock, R. C. Leegood, and M. Stitt. 1992. The effect of water stress on photosynthetic carbon metabolism in four species grown under field conditions. *Plant Cell and Environment* 15: 25–35.

Ramos-Diaz, A., L. Brito-Argaez, T. Munnik, and S. M. T. Hernandez-Sotomayor. 2007. Aluminum inhibits phosphatidic acid formation by blocking the phospholipase C pathway. *Planta* 225: 393–401.

Rengel, Z. 1992. Role of calcium in aluminum toxicity. *New Phytologist* 121: 499–513.

Rengel, Z., and D. C. Elliott. 1992. Mechanism of Al inhibition of net $^{43}Ca^{2+}$ uptake by *Amaranthus* protoplasts. *Plant Physiology* 98: 632–638.

Ryan, P. R., E. Delhaize, and P. J. Randall. 1995. Characterization of Al-stimulated efflux of malate from the apices of Al-tolerant wheat roots. *Planta* 196: 103–110.

Ryan, P. R., J. M. Ditomaso, and L. V. Kochian. 1993. Aluminium toxicity in roots: An investigation of spatial sensitivity and the role of the root cap. *Journal of Experimental Botany* 44: 437–446.

Ryan, P. R., and L. V. Kochian. 1993. Interaction between aluminum toxicity and calcium uptake at the root apex in near-isogenic lines of wheat (*Triticum aestivum* L.) differing in aluminum tolerance. *Plant Physiology* 102: 975–982.

Salisbury, E. 1962. The biology of garden weeds. Part II. *Journal of the Royal Horticultural Society* 87: 458–470.

Sarkunan, V., C. C. Biddappa, and S. K. Nayak. 1984. Physiology of aluminum toxicity in rice. *Current Science* 53: 822–824.

Scholl, L. V., W. G. Keltjens, E. Hoffland, and N. V. Breemen. 2005. Effect of ectomycorrhizal colonization on the uptake of Ca, Mg, and Al by *Pinus sylvestris* under aluminum toxicity. *Forest Ecology and Managment* 215: 352–360.

Schroeder, J. I. 1988. K^+ transport properties of K^+ channels in the plasma membrane of *Vicia faba* guard cells. *Journal of General Physiology* 92: 667–683.

Severi, A. 1997. Aluminum toxicity in *Lemna minor* L. Effects of citrate and kinetin. *Environmental and Experimental Botany* 37: 53–61.

Silva, I., T. Smyth, D. Moxley, T. Carter, N. Allen, and T. Rufty. 2000. Aluminum accumulation at nuclei of cells in the root tip. Fluoresence detection using lumogallion and confocal laser scanning microscopy. *Plant Physiology* 123: 543–552.

Sivaguru, M., F. Baluska, D. Volkmann, H. H. Felle, and W. J. Horst. 1999. Impacts of aluminum on the cytoskeleton of the maize root apex: Short-term effects on the distal part of the transition zone. *Plant Physiology* 119: 1073–1082.

Sivaguru, M., T. Fujiwara, J. Samaj, F. Baluska, Z. Yang, H. Osawa, T. Maeda, T. Mori, D. Volkman, and H. Matsumoto. 2000. Aluminum-induced 1–3-β-D-glucan inhibits cell-to-cell trafficking of molecules through plasmodesmata. A new mechanism of aluminum toxicity in plants. *Plant Physiology* 124: 991–1005.

Slaski, J. J. 1994. Differences in the metabolic responses of root tips of wheat and rye to aluminium stress. *Plant and Soil* 167: 167–171.

Tabaldi, L. A., F. T. Nicoloso, G. Y. Castro, L. D. Cargnelutti, J. F. Goncalves, R. Rauber, E. C. Skrebsky, M. R. C. Schetinger, V. M. Morsch, and D. A. Bisognin. 2007. Physiological and oxidative stress responses of four potato clones to aluminum in nutrient solution. *Brazilian Journal of Plant Physiology* 19: 211–222.

Tabuchi, A., and H. Matsumoto. 2001. Changes in cell wall properties of wheat (*Triticum aestivum*) roots during aluminum-induced growth inhibition. *Physiology Plantarum* 112: 353–358.

Tardieu, F., and W. J. Davies. 1993. Root-shoot communication and whole-plant regulation of water flux. In: *Water Deficits. Plant Responses from Cell to Community*, eds. J. A. C. Smith, and H. Griffiths, pp. 147–162. Oxford: Bios Scientific Publishers.

Teraoka, T., M. Kanek, S. Mori, and E. Yoshimura. 2002. Aluminum rapidly inhibits cellulose synthesis in roots of barley and wheat seedlings. *Journal of Plant Physiology* 159: 17–23.

Tester, M. 1990. Plant ion channels: Whole cell and single-channel studies. *New Phytologist* 114: 305–340.

Thornton, F. C., M. Schaedle, and D. L. Raynal. 1986. Effect of aluminum on the growth of sugar maple in solution culture. *Canadian Journal of Forest Research* 16: 892–896.

Wagatsuma, T., S. Ishikawa, H. Obata, K. Tawaraya, and S. Katohda. 1995. Plasma membrane of younger and outer cells is the primary specific site for aluminum toxicity in roots. *Plant and Soil* 171: 105–112.

Wagatsuma, T., M. Kaneko, and Y. Hayasaka. 1987. Destruction process of plant root cells by aluminium. *Soil Science and Plant Nutrition* 33: 161–175.

Wagner, H., F. Willer, R. Samtleben, and G. Boos. 1994. Search for the antiprostatic principle of stinging netle (*Urtica dioica*) roots. *Phytomedicine* 1: 213–224.

Wallace, S. U., and I. C. Anderson. 1984. Aluminum toxicity and DNA synthesis in wheat roots. *Agronomy Journal* 76: 5–8.

White, M. C., R. L. Chaney, and A. M. Decker. 1974. Differential varietal tolerance in soybean to toxic levels of zinc in Sassafras sandy loam. *Agronomy Abstracts* 1: 144–145.

Wilman, D., and J. A. Riley. 1993. Potential nutritive value of a wide range of grassland species. *Journal of Agricultural Science* 120: 43–49.

Wright, R. J. 1989. Soil aluminum toxicity and plant growth. *Communications in Soil Science and Plant Analysis* 20: 1479–1497.

Yamamoto, Y., Y. Kobayashi, and H. Matsumoto. 2001. Lipid peroxidation is an early symptom triggered by aluminum, but not the primary cause of elongation inhibition in pea roots. *Plant Physiology* 125: 199–208.

Yamamoto, Y., Y. Kobayashi, D. Rama, S. Rikiishi, and H. Matsumoto. 2002. Aluminum toxicity is associated with mitochondrial dysfunction and the production of reactive oxygen species in plant cells. *Plant Physiology* 128: 63–72.

Yasar, U., I. I. Ozyigit and M. Serin. 2010. Judas tree (Cercis siliquastrum L. subsp. siliquastrum) as a possible biomonitor for Cr, Fe and Ni in Istanbul (Turkey). *Romanian Biotechnological Letters* 15: 4979–4989.

Zelitch, I. 1971. *Photosynthesis, Photorespiration and Plant Productivity.* New York: Academic Press.

Zhang, H., Y. H. Li, L. Y. Hu, S. H. Wang, L. F. Q. Zhang, and K. D. Hu. 2008. Effects of exogenous nitric oxide donor on antioxidant metabolism in wheat leaves under aluminum stress. *Russian Journal of Plant Physiology* 55: 469–474.

Zhang, G. C., J. J. Slaski, D. J. Archambault, and A. G. J. Taylor. 1997. Alteration of plasma membrane lipids in aluminum resistant and aluminum sensitive wheat genotypes in response to aluminum stress. *Physiologia Plantarum* 99: 302–308.