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Effect of aluminum stress on mineral nutrition in rice cultivars differing in aluminum sensitivity

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ABSTRACT

The effects of aluminum (Al) stress on ion concentration and distribution were investigated in four rice cultivars (Aiwu and IKP, Al sensitive; IRAT112 and IR6023, Al resistant). Macro and micronutrient levels in plant tissues were markedly affected by Al and the magnitude of this effect depended on the cultivar group (Al resistance versus Al sensitivity) and on the concentration of Al in the nutrient solution. Al decreased Ca, P, K, Mg and Mn concentrations in shoot and K, Mg and Mn in root. It increased Ca and P in root and caused an increase in shoot and root Al contents. All these effects were observed in both cultivar groups, but were more apparent in Al sensitive ones. In conclusion, the results support the idea that, compared to the Al sensitive cultivars Aiwu and IKP, Al resistance in IRAT112 and IR6023 could be explained by a limited absorption and translocation of Al from root to shoot and could also be explained by a more efficient transport of Ca, P and Mn from root to shoot. These findings showed clearly that more than one mechanism may contribute to Al resistance in rice plants.

Key words: mechanism resistance, nutrients allocation, *oryza sativa*

Efeito do alumínio na nutrição mineral de cultivares de arroz diferindo na sensibilidade ao alumínio

RESUMO

Estudou-se o efeito do estresse causado pelo alumínio (Al) na concentração e distribuição de íons de quatro cultivares de arroz (Aiwu e IKP, sensíveis ao Al; IRAT112 e IR6023, resistentes ao Al) e se concluiu que sua presença afetou os níveis de macro e micronutrientes nos tecidos das plantas enquanto a amplitude desse efeito depende dos grupos das cultivares (Al resistente versus Al sensível) e da concentração de Al na solução nutritiva. A presença do Al diminuiu a concentração de Ca, P, K, Mg e Mn nas folhas, mas a aumentou em K, Mg e Mn nas raízes. O Al causou aumento da concentração de Ca e P nas raízes e aumentou a sua quantidade nas folhas e raízes; esses efeitos foram observados nos dois grupos das cultivares, embora de forma mais marcada nas cultivares sensíveis ao Al. Os resultados reforçam a idéia de que, comparativamente às cultivares sensíveis Aiwu e IKP, a resistência ao Al nas cultivares resistentes IRAT112 e IR6023, pode ser explicada por uma absorção limitada e translocação do Al das raízes para as folhas e, possivelmente, por um transporte mais eficiente de Ca, P e Mn das raízes para as folhas. Os resultados mostram que mais de um mecanismo pode contribuir para a resistência ao Al, em plantas de arroz.

Palavras-chave: mecanismo de resistência, alocação de nutrientes, *oryza sativa*

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INTRODUCTION

Aluminum toxicity is a major factor constraining crop performance on the acid solis that predominates under tropical climates (Barceló & Porchenrieder, 2002). Aluminum affects primarily the root system of plants, causing inhibition of root elongation and restricting absorption of mineral elements and water (Slaski,1994). This leads to reduced growth and mineral deficiencies in shoots and leaves (Foy, 1988). Al interferes with the uptake, transport and use of essential elements such as Ca, Mg, P, K and Fe, and according to Foy (1988), the ability to maintain higher root and shoot concentrations of macro and micro nutrients cations in the presence of Al has usually been associated with Al resistant cultivars. However, studies devoted to the influence of Al upon mineral nutrition in plants frequently gave contradictory results. In rice, for example, there is no consensus that aluminium resistance is associated with more efficient transport of Ca: Sivaguru & Paliwal (1993) observed that Al resistant cultivars accumulated more Ca in their shoots than Al sensitive ones, but Jan (1991) reported that the Al sensitive cultivar IR45 retained more Ca in shoots than the Al resistant cultivate BG35 and concluded that Ca transport from root to shoot is not affected by Al in the sensitive rice cultivate IR45. In wheat, it is not clear whether differences in Al sensitivity among cultivars are due to differences in Al accumulation in the root system. Some studies showed that wheat roots of Al resistant cultivars accumulate more Al than those of Al sensitive ones (Aniol, 1983), while other works indicate that Al accumulation is similar in both resistant and sensitive wheat cultivars (Pettersson & Strid, 1989; Zhang & Taylor, 1989). As a consequence of these inconsistent findings, several mechanisms of Al resistance have been proposed: i) resistant plants prevent excess of Al absorption by the roots (Fageria et al., 1988); ii) aluminium resistant species limit Al accumulation in roots and restrict its transport to shoots (Fageria & Carvalho, 1982); iii) aluminium resistance in some species coincides with more efficient uptake and transport of P and Ca (Andrew & Vandenberg, 1973; Fageria, 1985). It is important to note that the above mechanisms are not necessarily mutually exclusive, and that more than one mechanism may contribute to Al resistance in a plant.

Since the possible relationship between Al resistance and mineral nutrition in plants remains largely debated, the aim of the present work is to investigate the influence of Al on ion (Mg, Ca, P, K, Mn and Al) concentration and distribution in shoot and root of rice (*Oryza sativa*). The behaviour of four well-know cultivars, differing in Al sensitivity (Costa et al., 1997), has been compared in order to establish whether differences in resistance among these cultivars is associated with differences in macro and micronutrients allocation in plant parts.

MATERIAL AND METHODS

Seeds of I Kong Pao (IKP) and Aiwu (Al sensitive), obtained from WARDA (West Africa Rice Development Association, Senegal) and seeds of IRAT112 (IRAT), and IR6023-10-1-1 (IR) (Al resistant), obtained from IRRI (International Rice Research Institute, Philippines), were germinated in filter paper moistened with de-ionised water. When ten days old, plantlets were transferred to a phytotronic growth room. They were fixed on polystyrene plates floating on tanks containing 25 L of nutrient solution composed as follows: $MgSO_4.7H_2O$ (240.7 mg L^{-1}), NH_4NO_3 (228.6 mg L^{-1}), $Ca(NO_3)_2.4H_2O$ (41.02 mg L^{-1}), $FeSO_4.7H_2O$ (27.8 mg L^{-1}), KCl (16.09 mg L^{-1}) $NaH_2PO_4.2H_2O$ (6.16 mg L^{-1}), the micro elements according to Yoshida (1976), and $Al_2(SO_4)_{3\cdot 18H2O}$ at the concentration of 0 (control), 166, 333 and 500 mg L^{-1} (corresponding to 0, 500, 1000 and 1500 µM Al). The pH was adjusted to 3.85 ± 0.15 with HNO_3 and checked three times a week. Every week, the solutions were renewed and the tanks randomly rearranged. A 12 h daylength, at a minimum photon flux density of 200 µmol m^{-2} s^{-1}, was provided by Sylvania tubes. The temperature was 25-30/22-25 °C day per night, and the relative humidity was between 60 and 80%. After 40 days, five plants per treatment were harvested, and growth parameters were measured (Costa et al., 1997). Roots were rinsed for 1 min with $SrCl_2$ (1 mM) to remove ions from the free space. Shoots and roots were separately collected and oven-dried at 80 °C for 48 h. Dry matter was weighed before the samples were digested in HNO_3 (70% v/v). After total evaporation, minerals were solubilised in HCl (0.1 N). K, P, Mg, Mn, Ca, and Al contents were then analysed in both plant parts (shoots and roots) using an inductively coupled argon plasma emission spectrophotometer (Jobin-Yvon JY 48). The results obtained are expressed in µg/mg of dry weight. Rate of ion transport (RI) to shoot was calculated using the equation $RI = IS/IR$, where IS and IR are the amounts of ion in shoot and root respectively.

Two identical experiments were performed with similar results, thus pooled data is reported in this paper. The statistical analyses (ANOVA) were conducted with absolute values, using the Al concentration and the cultivate or the group of cultivars (Al resistant versus Al sensitive) as variables. The threshold for statistically significant differences was $P < 0.05$.

RESULTS AND DISCUSSION

Aluminum

Al stress caused an increase in root and shoot Al content, being greater in Al sensitive IKP and Aiwu than in Al resistant cultivars at the high Al doses (1000 and 1500 µM) (Figure 1A; Figure 1B).

The Al shoot/root ratio, which is an indicator of Al translocation from root to shoot, was always lower in Al resistant than Al sensitive cultivars (Table 1).

Statistical analyses showed that Al concentration significantly affected Al contents in roots and shoots and this parameter can also be used to discriminate between genotypes and group of Al-resistant and Al-sensitive genotypes. The interactions between Al concentration and genotype and group of genotypes were always significant (Table 2; Table 3).

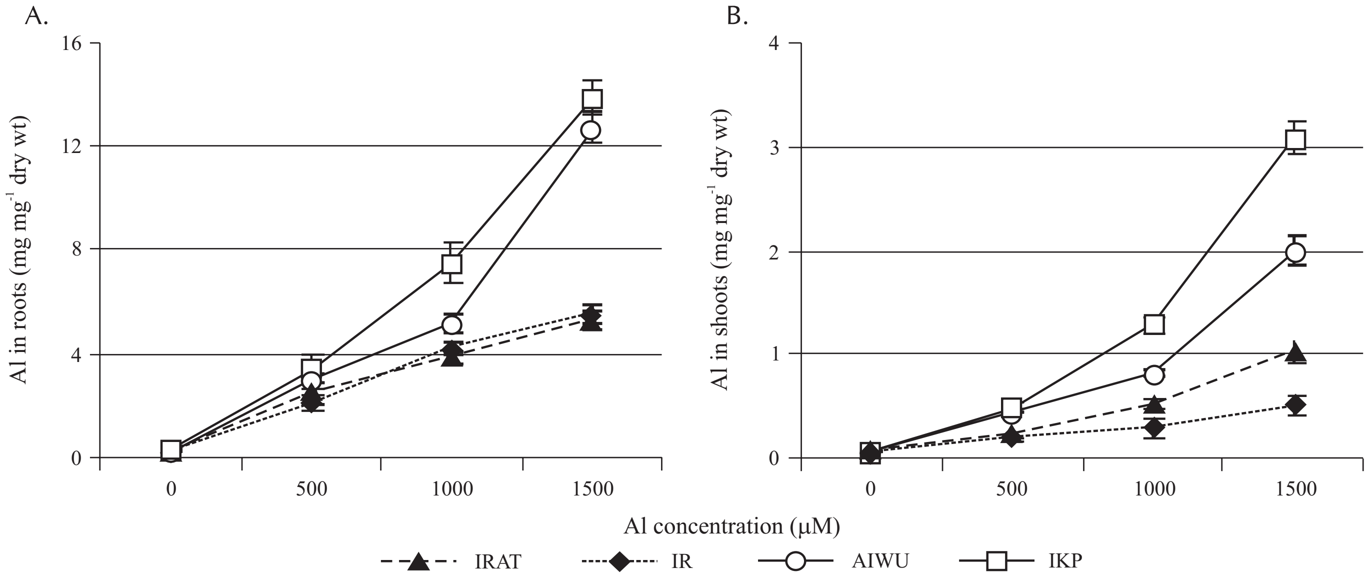

Figure 1. Effect of Al stress on Al content in roots (A) and shoots (B) of two Al resistant (IRAT and IR) and two Al sensitive (Aiwu and IKP) rice cultivars

The Al concentration in roots and shoots of all cultivars increased with increasing Al concentration in the nutrient solution and was always found to be far higher in roots than in shoots. These results confirm that Al mobility in rice is relatively low, as was already pointed out by Jan & Pettersson (1989). Similar results were reported for other species including wheat (Scott et al., 1992), maize (Guevara et al., 1992) and beech (Balsberg-Pahlsson, 1990).

Table 1. Shoot/Root values of ion content in two Al-resistant (IRAT and IR) and two Al-sensitive (Aiwu and IKP) rice cultivars exposed to different Al treatments during 40 days of hydroponic crop. Control: Al 0; Al data pooled for the two highest Al doses (1000 and 1500 mM). Statistical analysis (ANOVA) of differences between controls and Al treatments

	Al	Ca	P	K	Mg	Mn
			IRAT			
Control	–	14.43	0.85	5.92	18.3	44.33
Al	0.34	13.48 ns	0.67 *	7.89 *	19.8 ns	20.62 *
			IR			
Control	–	13.65	0.97	4.85	18.74	61.74
Al	0.29	13.70 ns	0.77 *	6.35 *	16.92 ns	32.16 *
			Aiwu			
Control	–	19.04	0.75	6.70	19.59	52.66
Al	0.63	06.40 *	0.33 *	7.75 *	18.20 ns	12.53 *
			IKP			
Control	–	15.36	0.800	7.90	19.85	56.89
Al	0.87	04.56 *	0.270 *	8.87 *	20.14 ns	11.03 *

* significant at the 0.05 level; ns no significant

Differential Al tolerance among certain plant species and cultivars has been correlated with their differential accumulation of Al (Fageria & Carvalho, 1982). At root and shoot levels, strong differences among cultivars were recorded for the accumulation of this toxic ion. The Al resistance of IRAT and IR was clearly related to the restriction of Al absorption by the roots, since these cultivars accumulated less Al in their roots and shoots than Al sensitive ones. It has been already reported that resistant plants either prevent excess Al absorption by the roots or detoxify Al after it has been absorbed (Fageria et al., 1988). Al resistance in IRAT and IR was also associated to a restriction of Al translocation from root to shoot as shown by Al shoot/root ratio (Table 1). Similar findings were already reported for rice (Fageria & Carvalho, 1982; Jan & Pettersson, 1989) and maize (Guevara et al., 1992). The results of this research suggest that in rice, Al exclusion and internal mechanisms of detoxification could exist simultaneously to avoid and/or to tolerate Al at root level. However, there is a large discussion in the literature

Table 2. Effect of Al concentration and genotype or group of genotypes (Al-resistant vs. Al-sensitive) and interactions, among different ions concentrations in the roots collected after 40 days of hydroponic crop. Results of ANOVA (F values)

Parameter	Source of variability				
	Al concentration	Genotype	Group of genotypes	Interation Al X genotype	Interation Al X group genotypes
Al	36.650 ***	6.666 **	19.499 ***	2.661 **	7.918 ***
Ca	1.611 ns	2.165 ns	6.807 *	1.129 ns	3.178 *
K	34.671 ***	30.399 ***	20.331 ***	5.902 ***	8.399 ***
Mn	0.774 ns	11.598 ***	2.930 ns	1.340 ns	2.498 ns
Mg	79.431 ***	18.792 ***	28.662 ***	7.763 **	1.791 ns
P	12.419 ***	5.222 *	14.139 **	1.430 ns	3.818 *

* significant at the 0.05 level; ** significant at the 0.01 level; *** significant at the 0.001 level; ns no significant

Table 3. Effect of Al concentration and genotype or group of genotypes (Al-resistant vs. Al-sensitive) and interactions, among different ions concentrations in the shoots collected after 40 days of hydroponic crop. (F values)

Parameter	Source of variability				
	Al concentration	Genotype	Group of genotypes	Interation Al X genotype	Interation Al X group genotypes
Al	52.500 ***	19.149 ***	39.763 ***	6.888 ***	15.452 ***
Ca	38.398 ***	9.843 ***	27.771 ***	2.697 ns	4.904 *
K	6.955 **	21.862 ***	22.072 ***	3.530 **	7.006 **
Mn	49.483 ***	29.151 ***	32.947 ***	9.723 ***	9.985 ***
Mg	80.832 ***	18.546 ***	10.067 **	3.780 *	1.225 ns
P	22.209 ***	5.072 *	14.250 **	3.055 *	5.238 **

* significant at the 0.05 level; ** significant at the 0.01 level; * significante cant at the 0.001 level; ns no significant

whether the Al concentration in roots could be associated with Al resistance. In wheat, the most studied species in this respect, it is not possible to decide whether differences in Al sensitivity among cultivars are due to differences in Al accumulation in the root system or not: some studies showed that roots of Al resistant cultivars accumulate more Al than roots of Al sensitive ones (Aniol, 1983), while other works indicate that Al accumulation is similar in both resistant and sensitive cultivars (Pettersson & Strid, 1989, Zhang & Taylor, 1989). It is possible that the lack of correlation among Al sensitivity and Al concentration in the root tissue may be due to the fact that the technique used for Al analyses in whole roots can not allow the separation of the free Al (ie. toxic) from the Al detoxified by the roots.

Macro nutrients

Al stress induced an increase in root Ca and P contents in the Al sensitive cultivars confronted to 1000 and 1500 µM of Al, except for P in root of Aiwu at 1000 mM of Al (Figure 2A; Figure 2B). In the resistant cultivars, however, there was no significant effect on these ions, except for a slight increase in P content in root of IR (Figure 2A; Figure 2B). Al concentration significantly affected P contents in roots and this parameter can also be used to discriminate between genotypes and group of Al-resistant and Al-sensitive genotypes. The interactions among Al concentration and group of genotypes were always significant. This was not the case when interactions among Al concentration and genotype were considered (Table 2). At the shoot level, Ca and P contents decreased in

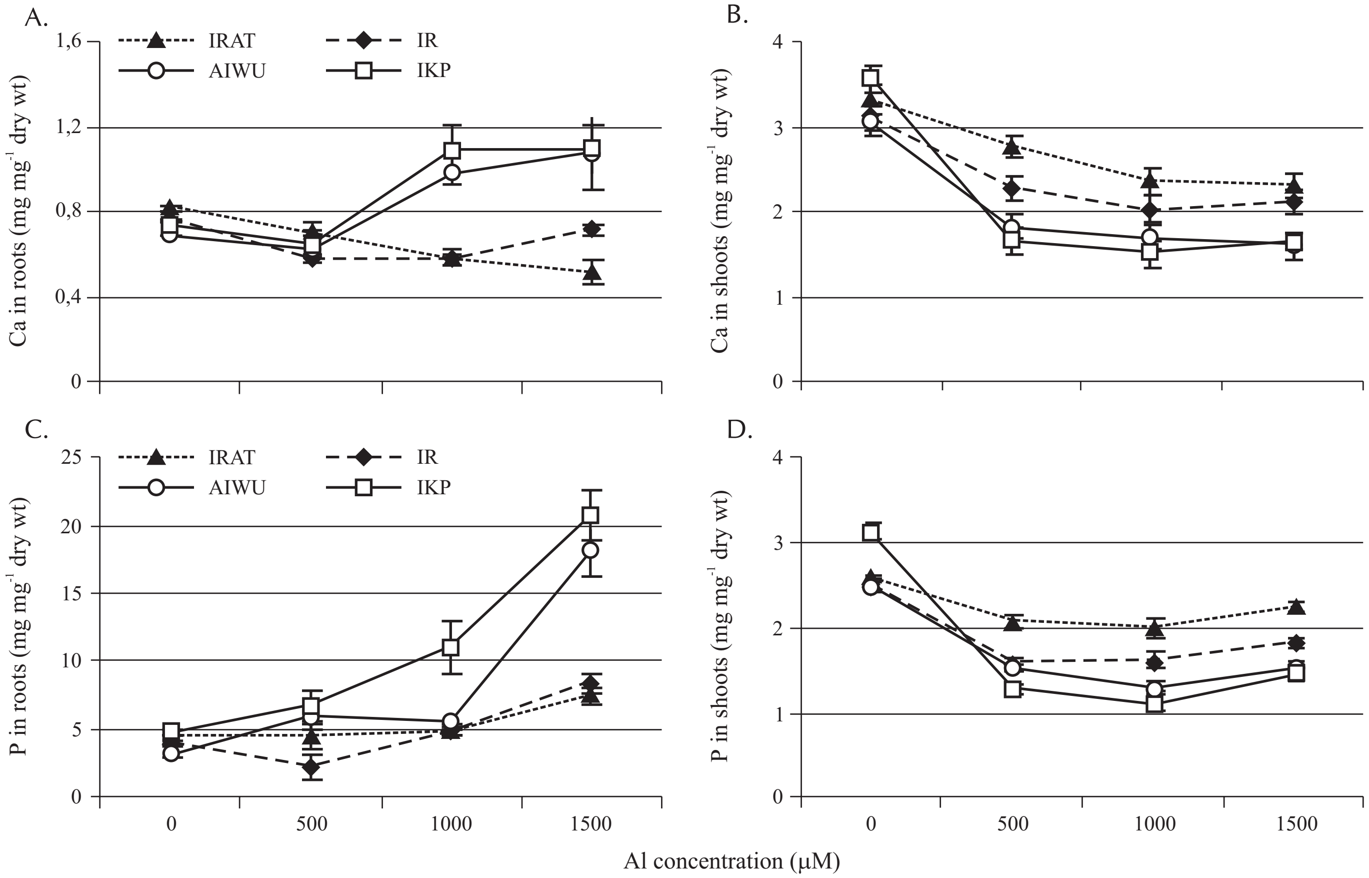

Figure 2. Effect of Al stress on Ca (A, B) and P (C, D) content in roots and shoots of two Al resistant (IRAT and IR) and two Al sensitive (Aiwu and IKP) rice cultivars

all cultivars (Figure 2C; Figure 2D). The decrease was more pronounced in sensitive cultivars than in resistant ones. As a consequence, Ca translocation to the shoots decreased in response to Al stress only in Al sensitive cultivars (Table 1). The P translocation decreased in all cultivars (Table 1). However, this effect was always more marked in Aiwu and IKP than in Al resistant IRAT and IR. Al concentration significantly affected Ca and P contents in shoots and this parameter can also be used to discriminate among genotypes and group of Al-resistant and Al-sensitive genotypes. The interactions among Al concentration and group of genotypes were always significant. This was not the case when interactions among Al concentration and genotype were considered for Ca contents (Table 3).

Al at 1500 µM caused a decrease in K contents in roots of all cultivars (Figure 3A). In shoot, K content was markedly reduced by all Al treatments in IKP and at the highest dose only in Aiwu. In the resistant cultivars, Al stress had no significant effect on K content of shoot (Figure 3B). The increased K shoot/root ratio observed in all cultivars in response to Al stress (Table 1) was due to a decrease in K absorption by the roots. Statistical analyses showed that Al concentration significantly affected K contents in roots and shoots and this parameter can also be used to discriminate among genotypes and group of Al-resistant and Al-sensitive genotypes. The interactions among Al concentration and genotype and group of genotypes were always significant (Table 2; Table 3).

All cultivars showed a significant decrease in root and shoot Mg contents at all Al doses (Figure 3C; Figure 3D). Al stress had no significant effect on the proportion of Mg translocated (Table 1), but decreased the absorption of this element.

At high Al doses (1000 and 1500 µM), Al resistance of the two rice cultivars IRAT and IR coincided with more efficient transport of Ca and P from root to shoot (Table 1). The increase in root P content associated with a decrease in shoot P content in Al sensitive cultivars Aiwu and IKP might be due to the formation of Al and P complexes inside the plant root, thus rendering part of the P unavailable for translocation within the plant (Sivaguru & Paliwal, 1993). In rice (Fageria, 1985; Jan, 1991; Sivaguru & Paliwal, 1993), wheat (Miranda & Rowell, 1989) and in certain pasture species (Andrew & Vandenberg, 1973), differential Al resistance has been correlated with differential abilities to absorb, to translocate and to utilise P in the presence of Al. Exposure to Al did not affect P concentration in root of Al-resistant *Brachiaria* cultivar, but it caused a 70% decline in P content of Al-sensitive *Brachiaria* cv (Wenzel et al., 2002). The question as to whether a more efficient transport of Ca in plants is associated with Al resistance is still unsolved. In this study, Ca translocation decreased in response to Al stress in Al sensitive cultivars Aiwu and IKP, a result that is in agreement with the findings of Sivaguru & Paliwal (1993), but not with the observations of Jan (1991). These discrepancies are unexplained

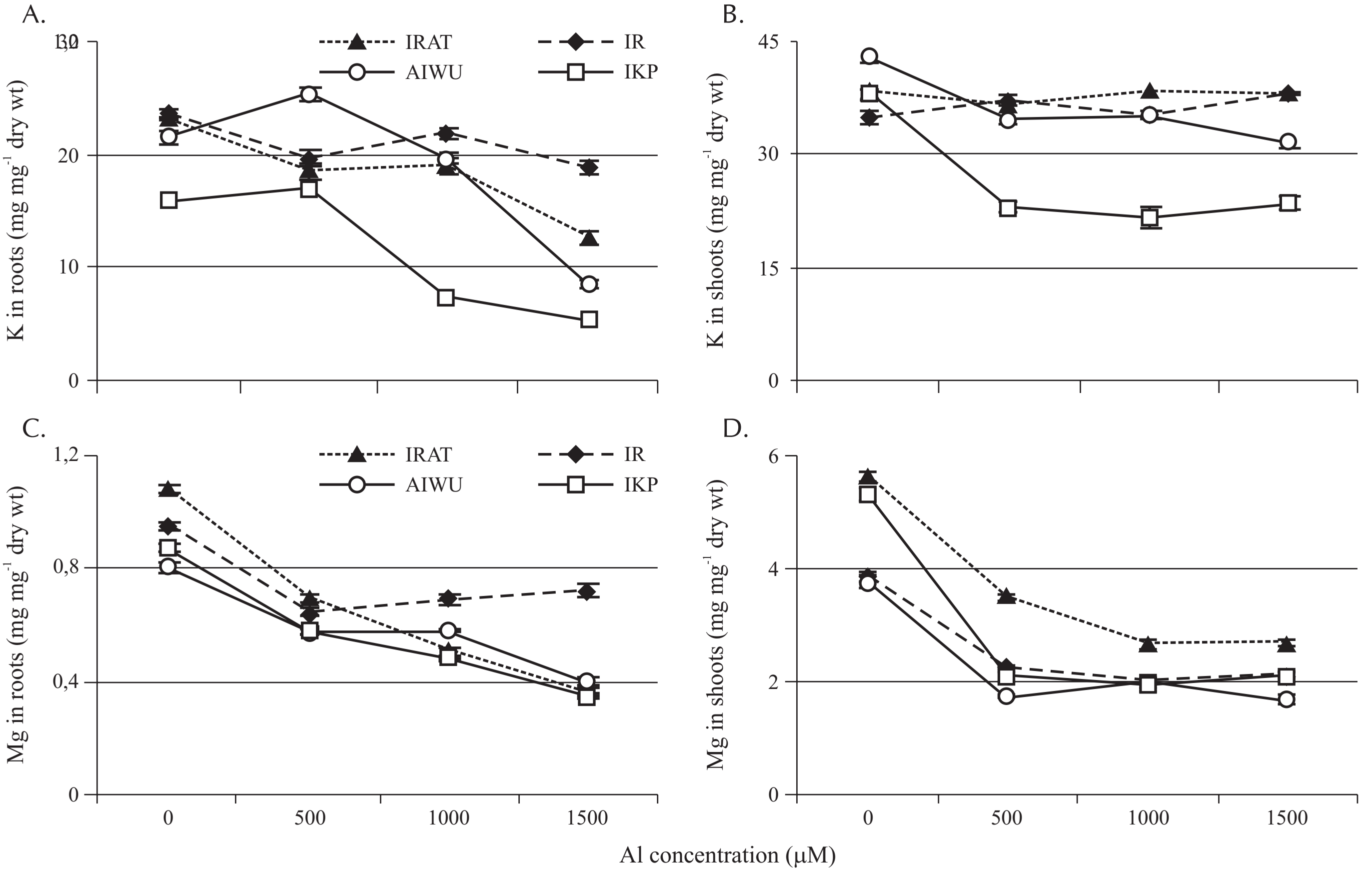

Figure 3. Effect of Al stress on K (A, B) and Mg (C, D) content in roots and shoots of two Al resistant (IRAT and IR) and two Al sensitive (Aiwu and IKP) rice cultivars

but could be due to differences in cultivate behaviour. Al resistance in certain cultivars of wheat, barley and soybean has been associated with their ability to cope with Al induced Ca deficiency or with a limited Ca translocation (Fageria et al., 1988). Conversely, Edward & Horton (1977) pointed out that aluminium toxicity in peach was not related to inhibition in translocation of Ca. It seems that, in some species and cultivars, efficient transport of Ca constitutes a complementary mechanism of aluminium resistance. Moreover, high concentrations of Ca in the solution at appropriate Al/Ca ratios could increase chlorophyll content, an indication of alleviation effect in mungbean (Yang et al., 2001). In the presence of high Al doses (1500 µM), K content in root of all cultivars showed a significant decrease that corresponds to a decrease in K absorption by the roots. In spite of a decrease in shoot K content of Al sensitive cultivars, no correlations among K content and differential Al resistance among the rice cultivars could be established, since, irrespective of Al doses, except for 1500 µM, Aiwu (Al sensitive) and the Al resistant (IRAT and IR) cultivars behaved similarly in the presence of aluminium. In rice, Jan (1991) observed that Al did not have a significant effect on shoot K content but increased root K content in all cultivars. However, this effect is not linked to differences in Al sensitivity. The finding that Al induced a decrease in root and shoot Mg contents of the rice cultivars tested in this work agrees with other observations on rice (Fageria & Carvalho, 1982; Sarkunan & Biddappa, 1982; Jan, 1991) and wheat (Scott et al., 1992; Moustakas et al., 1995). This decrease in Mg irrespective of rice cultivars correspond to a decrease in Mg absorption and indicates a general Al effect rather than differential Al resistance, as has already been suggested for rice (Jan, 1991). Al-induced Mg deficiency has been associated with inhibition of Mg uptake (Huang et al., 1992) by blocking binding sites of transport proteins (Rengel & Robinson, 1989). However, in sugar maple, higher levels of Al reduced Mg concentration in leaves has caused root and foliar injury, but no negative effects of Al on growth were observed (Schier & McQuattie, 2002).

Micro nutrients

In the presence of 1500 µM, Al decreased Mn content in root of IKP (Figure 4A). Irrespective of Al doses, shoot Mn content decreased (Figure 4B) and as a consequence, Mn translocation decreased in response to Al stress. The decrease was more pronounced in Al sensitive cultivars than in Al resistant ones (Table 1).

The decrease in shoot Mn content was more marked in Al sensitive cultivars than in Al resistant ones. The relation between Mn in both shoot and root (Table 1) seems to indicate that Al sensitive cultivars have a system of translocation that is more affected than in Al resistant ones, and this might be a contributing factor to explain their susceptibility to Al. In rice, Jan (1991) observed that Al toxicity in sensitive cultivars was related to a reduction of Mn status in the shoot in conjunction with reduced Mn uptake rates in the root.

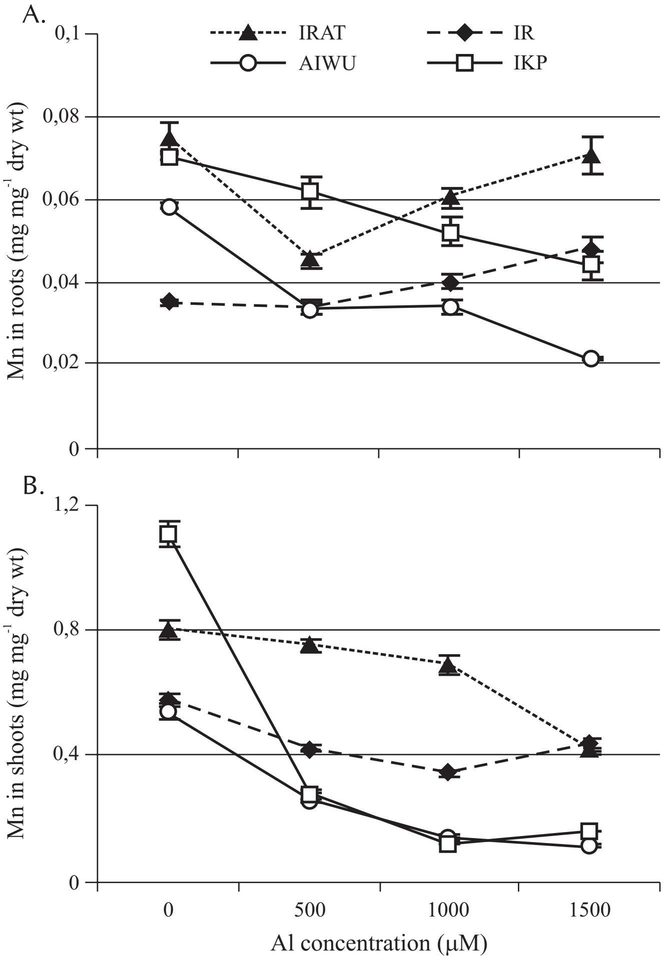

Figure 4. Effect of Al stress on Mn content in roots (A) and shoots (B) of two Al resistant (IRAT and IR) and two Al sensitive (Aiwu and IKP) rice cultivars

CONCLUSION

1. The data presented here show that in rice, the concentration of macro and micronutrients in plant tissues were markedly affected by Al and the magnitude of this effect depends on cultivar group (Al resistant versus Al sensitive) and, in some instances, on Al concentration.

2. In conclusion, these results support that, comparatively to the sensitive cultivars, the Al resistance in IRAT and IR could be explained by a limited absorption and translocation of Al from root to shoot. The macro and micronutrients concentrations could explain partly the differential Al resistance among cultivars: Al resistance of the two rice cultivars IRAT and IR could also be explained by a more efficient transport of Ca, P and Mn from root to shoot. These findings showed clearly that more than one mechanism may contribute to Al resistance in rice plants.

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