Amer. J. Bot. 72(5): 695–701. 1985.

MECHANISMS OF ALUMINUM TOLERANCE IN TRITICUM AESTIVUM L. (WHEAT). I. DIFFERENTIAL PH INDUCED BY WINTER CULTIVARS IN NUTRIENT SOLUTIONS[1]

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ABSTRACT

Twenty winter cultivars of *Triticum aestivum* L. (wheat) were grown in solution culture with and without aluminum (Al) (74 μM, 2.0 mg L^{-1}) for 14 days. Exposure to Al increased root growth of the most tolerant cultivar, while both root and shoot growth were depressed in all other cultivars. On the basis of a root tolerance index (RTI = weight of roots grown with Al/ weight of roots grown without Al), cultivar tolerance to Al ranged 9-fold, from 0.13 ± 0.01 to 1.16 ± 0.10. Symptoms of Al toxicity were most evident on roots. Aluminum-affected roots were relatively short and thick and had numerous undeveloped laterals. Leaves of some cultivars showed chlorosis resembling iron deficiency, and others showed purple stems typical of phosphate deficiency.

Plants of all cultivars grown with and without Al depressed the pH of nutrient solutions, presumably until NH_4^+ was depleted, at which point the pH increased. Cultivar tolerance, expressed both as the root tolerance index and a shoot tolerance index, was negatively correlated with the negative log of the mean hydrogen ion (H^+) concentration, the minimum pH, and the slope of the pH decline, each calculated from pH data collected during the first 9 days of the experimental period before any sharp rises in pH occurred. These results are consistent with the hypothesis that the Al tolerance of a given cultivar is a function of its ability to resist acidification of the nutrient solution and hence to limit the solubility and toxicity of Al.

DIFFERENTIAL tolerance to aluminum (Al) among cultivars of *Triticum aestivum* L. (wheat) has been reported at least 35 times in the literature, yet the mechanism for such tolerance remains obscure. The hypothesis that plant-induced pH of the rhizosphere determines cultivar tolerance to Al has generated considerable investigation. Foy et al. (1965b) first demonstrated that an Al-tolerant cultivar of *T. aestivum* was able to induce a higher pH in nutrient solutions than an Al-sensitive cultivar when both were grown with and without Al. Changes in solution pH were thought to reflect greater pH changes in the rhizosphere. Foy et al. (1965b) also demonstrated similar pH differences in soil experiments. Because the solubility of Al decreases rapidly in the range of 4.0 to 5.0, Foy et al. (1965b) hypothesized that plants maintaining a relatively high rhizosphere (nutrient solution) pH may decrease the solubility and hence the toxicity of Al. In contrast, plants maintaining a relatively low rhizosphere (nutrient solution) pH may be exposed to higher concentrations of soluble Al, and hence greater toxic effects would be manifest.

A relationship between Al tolerance and the ability of a cultivar to maintain a relatively high pH in the growth medium has been demonstrated for *T. aestivum* (Fleming, 1983; Foy and Fleming, 1978, 1982; Mugwira and Elgawhary, 1979; Mugwira, Elgawhary and Patel, 1976, 1978; Mugwira and Patel, 1977; Foy et al., 1967; and Dodge and Hiatt, 1972), × *Triticosecale* (triticale), *Secale cereale* (rye) (Mugwira and Patel, 1977; Mugwira et al., 1976), *Hordeum vulgare* (Foy et al., 1967), and *Pisum sativum* (pea) (Klimashevskii and Dedov, 1977; Klimashevskii and Bernatskaya, 1973). However, some basic issues concerning the plant-induced pH hypothesis remain unresolved. For example, differences in plant-induced pH between cultivars of *T. aestivum* observed by Foy and Fleming (1982), Mugwira and Elgawhary (1979), Mugwira et al. (1976, 1978), and Foy

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[1] Received for publication 7 May 1984; revision accepted 28 January 1985.

Financial support for Dr. Taylor was provided by the Natural Sciences and Engineering Research Council of Canada. We thank Dr. D. H. Smith and Dr. L. W. Briggle for aid in selection of cultivars and provision of seed material, and Dr. R. B. Clark, Dr. A. A. Crowder, A. L. Fleming, Dr. D. T. Krizek, and Dr. E. H. Lee for review of the manuscript.

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TABLE 1. *Differential Al tolerance of 20 winter cultivars of* T. aestivum *grown in nutrient solutions as measured by the root tolerance index (RTI) and shoot tolerance index (STI)*

Variety	Mean RTI ± SE	Variety	Mean STI ± SE
Atlas-66	1.16 ± 0.10a	Atlas-66	0.97 ± 0.03a
Logan	0.82 ± 0.09b	Centurk	0.85 ± 0.03ab
Seneca	0.76 ± 0.04b	Logan	0.85 ± 0.10ab
Titan	0.72 ± 0.10bc	Monon	0.85 ± 0.05ab
Druchamp	0.58 ± 0.02cd	Druchamp	0.83 ± 0.01abc
Blueboy	0.52 ± 0.02d	Seneca	0.82 ± 0.02abcd
Lucas	0.50 ± 0.07d	Titan	0.79 ± 0.12bcde
Centurk	0.46 ± 0.04de	Blueboy	0.79 ± 0.02bcde
Benhur	0.44 ± 0.01de	Arthur-71	0.79 ± 0.06bcde
Arthur-71	0.43 ± 0.10de	Redcoat	0.78 ± 0.08bcde
Monon	0.43 ± 0.06de	Abe	0.75 ± 0.05bcde
Reed	0.42 ± 0.02de	Benhur	0.74 ± 0.03bcde
Riley-67	0.30 ± 0.04ef	Triumph	0.74 ± 0.04bcde
Abe	0.22 ± 0.05f	Lucas	0.73 ± 0.05cde
Triumph	0.21 ± 0.04f	Larned	0.70 ± 0.01cde
Redcoat	0.20 ± 0.04f	Riley-67	0.69 ± 0.01cde
Eagle	0.20 ± 0.02f	Eagle	0.68 ± 0.02cde
Larned	0.18 ± 0.02f	Sage	0.66 ± 0.04de
Sage	0.18 ± 0.04f	Reed	0.66 ± 0.01de
Scout	0.13 ± 0.01f	Scout	0.64 ± 0.02e

Note: Data presented as the mean RTI and STI ± standard error. Means followed by the same letter are not significantly different at the 5% level according to Duncan's Multiple Range Test.

et al. (1967) were correlated with cultivar tolerance to Al. However, these pH differences had occurred after 10–12 days of growth, after depletion of NH_4^+ from nutrient solutions and the accompanying rapid rise in pH. Such pH changes may have been an effect, rather than the cause of differential Al tolerance. This could be true if differential tolerance to Al by a different mechanism affected both the rate at which NH_4^+ was depleted from nutrient solutions and the time required for the rapid rise in pH. One might then ask the question, can differential Al tolerance, which is apparent visually after 3–5 days treatment, be correlated with pH changes in nutrient solutions occurring prior to NH_4^+ depletion?

Another issue arises because the relationship between Al tolerance and pH of the growth medium has been established using either Al-tolerant and Al-sensitive pairs of cultivars (Fleming, 1983; Foy and Fleming, 1978, 1982; Foy et al., 1965b, 1967), or a limited number (3 or 4) of cultivars (Mugwira and Patel, 1977; Mugwira et al., 1976). If the plant-induced pH hypothesis is correct, this relationship should hold over a broad range of Al tolerance, yet this has yet to be demonstrated. The objectives of this study were to test for a continuous relationship between tolerance to Al and plant-induced pH of nutrient solutions prior to NH_4^+ depletion, using 20 cultivars of *T. aestivum.*

MATERIALS AND METHODS—Twenty winter cultivars of *T. aestivum* (Table 1) were selected to represent a known range of Al tolerance or because they were commonly used for wheat production in the United States in 1979 (Briggle et al., 1982). Seeds of each cultivar were germinated in aerated, deionized water for 24 hr; seedlings were grown on cheesecloth in deionized water for 3 days and allowed to elongate for 5 days on plexiglass support frames in dilute nutrient solutions containing the following: 1.27 Ca, 0.27 Mg, 3.32 NO_3^--N, and 0.24 NH_4^+-N in mM.

Twenty-four uniform, 9-day-old seedlings from each cultivar were mounted on the covers of 8-L polyethylene containers. Each container supported 12 plants in four bunches of 3 plants each. The nutrient solutions were a modification of that used by Foy et al. (1967) and contained the following nutrients: 3.71 NO_3^--N, 0.30 NH_4^+-N, 1.27 Ca, 0.75 K, 0.27 Mg, 0.12 SO_4^{2-}-S, 0.10 HPO_4^{2-}-P in mM, and 58.5 Cl, 53.9 Na, 17.9 Fe, 6.6 B, 2.4 Mn, 0.6 Zn, 0.2 Cu, and 0.1 Mo in μM. In contrast to Foy et al. (1967), Fe was supplied as FeHEDTA (ferric hydroxyethylethylene-diaminetriacetate) prepared from equimolar amounts of $FeCl_3$ and Na_3HEDTA. Growth containers were covered to inhibit algal growth.

Plants were grown in a controlled environment room at 23 ± 1 C for a 16-hr light period and at 19 ± 1 C during darkness. Relative humidity was not controlled but averaged 51 ± 5% during the light period and 93 ± 8% during darkness. The growth room was illuminated by 84 fluorescent (1,500 mA) and 40 incan-

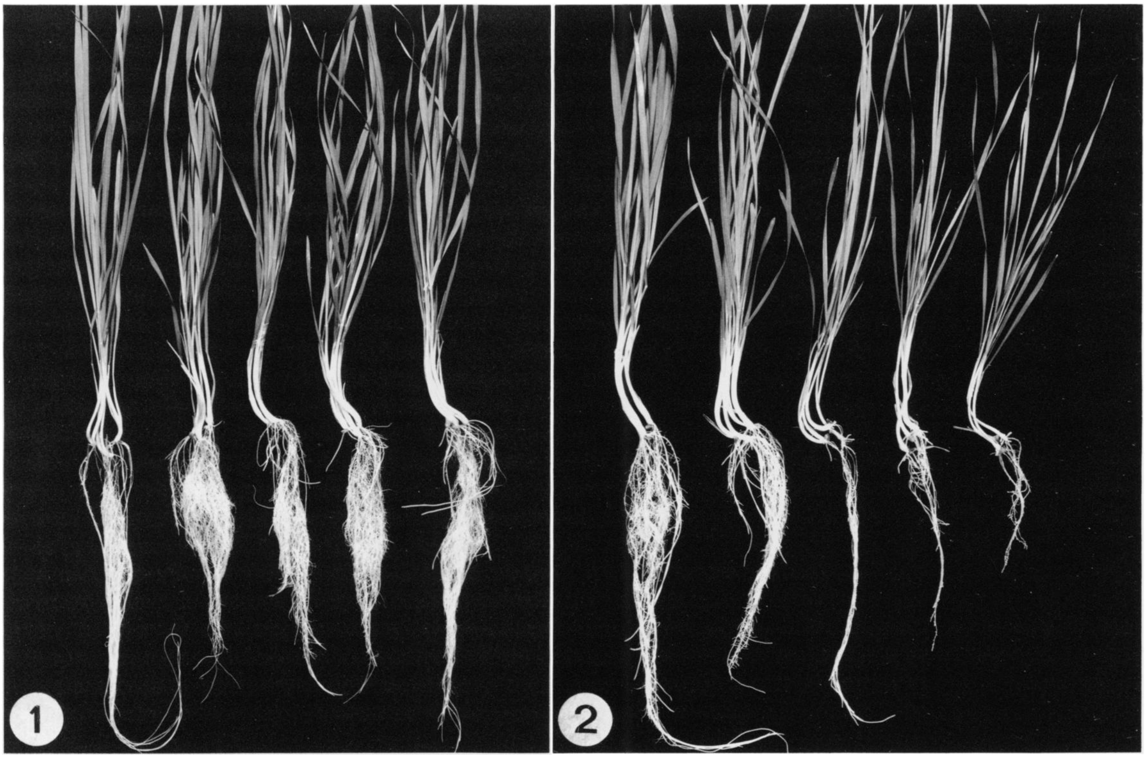

Fig. 1, 2. **1.** Relative growth of five winter cultivars of *T. aestivum* grown without Al. Cultivars from left to right are Atlas-66, Logan, Centurk, Riley-67, and Scout. **2.** Relative growth of five winter cultivars of *T. aestivum* grown with Al (74 μM, 2.0 mg L^{-1}). Cultivars from left to right are Atlas-66, Logan, Centurk, Riley-67, and Scout.

descent lamps (60 w) located 0.9 m above the plant bases. The level of photosynthetically active radiation (PAR) was 190 ± 13 μmol s^{-1} m^{-2} at plant base level and increased to 230 ± 18 μmol s^{-1} m^{-2} at the top of the leaf canopy (40 cm). Although not controlled, solution temperatures were 22 ± 2 C at the end of the light period and 20 ± 1 C at the end of darkness.

A randomized block, factorial design, with 20 cultivars, two treatments, and three replicates (120 containers) was used. Due to space constraints, replication was achieved in time (external replication). Control and Al treatments within each replicate were blocked together to minimize variation. Treatments included the control (no added Al) and 74 μM (2.0 mg L^{-1}) Al, supplied as $AlK(SO_4)_2$ $12H_2O$. This level of Al was selected to provide adequate separation of cultivars on the basis of tolerance to Al (Foy et al., 1965b, Foy and Fleming, 1982). The pH of nutrient solutions was adjusted initially to 4.5 with HCl or KOH and was measured daily.

After 14 days of treatment, plants were harvested, divided into roots and shoots, rinsed four times in distilled water, dried to constant weight at 60 C, and weighed. A root tolerance index (RTI) and a shoot tolerance index (STI) were calculated by dividing the root or shoot yield of plants grown with Al by the root or shoot yield of plants grown without Al. The ability of the plants to alter the pH of nutrient solutions was evaluated by the negative log of the mean H^+ concentration, the minimum pH, and the slope (rate) of the pH change, each determined from the first 9 days of the experiment before any sharp rises in solution pH occurred.

Statistical analyses of the data were performed using simple regression, Duncan's Multiple Range Test, and descriptive statistics available on the Statistical Analysis System (SAS) version 79.6 (SAS Institute, Inc., 1982). Significance was defined at the 95% confidence level.

RESULTS—The 20 winter cultivars of *T. aestivum* differed in their tolerance to Al. Exposure to Al increased the root growth of the most tolerant cultivar (Atlas-66), while both root and shoot growth were depressed in all other

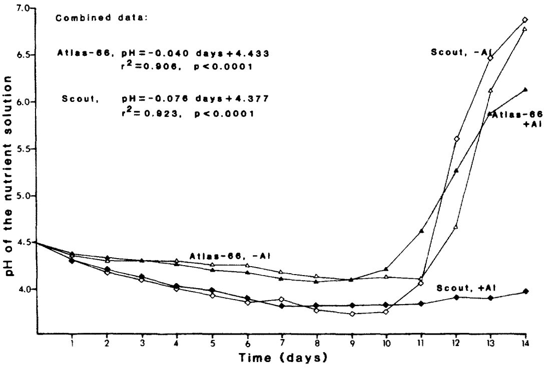

Fig. 3. Daily pH changes in nutrient solutions induced by an Al-tolerant cultivar, Atlas-66 (triangles), and an Al-sensitive cultivar, Scout (diamonds), of *T. aestivum* grown with Al (74 μM, 2.0 mg L^{-1}, solid symbols) and without Al (open symbols). Regression equations describe the relationship between pH of nutrient solutions and time for the first 9 days of the experimental period, prior to the pH rise.

cultivars (Table 1, Fig. 1, 2). Symptoms of Al toxicity were most evident on roots. Aluminum-affected roots were relatively short, thick, and had numerous undeveloped laterals. Leaves of some cultivars showed chlorosis resembling iron deficiency, and others showed purple stems typical of phosphate deficiency (Foy and Brown, 1964).

Ranking of the cultivars for tolerance to Al varied between the RTI and STI. Classifying plants on the basis of the RTI, the Al tolerance of the 20 cultivars ranged from 0.13 ± 0.01 to 1.16 ± 0.10. In contrast, the range of STI values was less, from 0.64 ± 0.02 to 0.97 ± 0.03. While the actual rankings by the two tolerance indices were not the same, the trends were similar.

Plants of each cultivar grown with and without Al induced a progressive decline in solution pH from the outset of the experiment until Days 10–12. Thereafter, the solution pH induced by each cultivar grown without Al, and the more Al-tolerant cultivars grown with Al, increased rapidly (Fig. 3). Differences in pH patterns between treatments, within cultivars, were not observed; hence, the treatments were grouped and the nature of the pH decline was evaluated. For each cultivar, the pH decline prior to the rapid rise in pH was explained by a linear model, although this could be misleading because pH itself is a logarithmic variable.

The relationship between tolerance to Al and pH of nutrient solutions was analyzed by simple regression with the RTI or STI as the independent variable and the negative log of the mean H^+ concentration, minimum pH, or slope of the pH decline as the dependent variables. Except with STI as the independent variable in Replicate 1, both the RTI and STI were significantly correlated with each of the pH variables (Table 2).

The pH variables were more closely related to the RTI than the STI, which is consistent with the fact that Al primarily affects root growth. For this reason, only the RTI results are discussed further. With the three replicates combined, the RTI was significantly correlated with the negative log of the mean H^+ concentration ($r^2 = 0.656$, $P < 0.0001$, Fig. 4), followed by minimum pH ($r^2 = 0.494$, $P < 0.0001$), and the slope of the pH decline ($r^2 = 0.436$, $P < 0.0001$) (Table 2). In each case, tolerance to Al was associated with the ability of the cultivar to resist acidification of the nutrient solution. Some variation between replicates was evident; hence, the explained variance in each of the combined analyses was generally lower than the variance explained when the replicates were analyzed individually (Table 2). Despite this variation, there was good agreement between replicates for the Al tolerance–nutrient solution pH relationship.

Discussion—The results of this and previous investigations show that root growth is more severely affected by Al than shoot growth (Aniol and Kaczkowski, 1979; Campbell and Lafever, 1976; Mugwira et al., 1976; Foy et al., 1965b, 1967, 1974; Kerridge, Dawson and Moore, 1971). Thus, it is not surprising that the RTI values had a greater range and were more closely related to the pH variables than STI. The STI was a less precise measurement of Al tolerance.

Using the RTI, the classification of the cultivars as Al-sensitive or Al-tolerant was in general agreement with a number of previous reports (Wallace, Henning and Anderson, 1982; Campbell and Lafever, 1976, 1981; Mugwira et al., 1976, 1978, 1981; Mugwira and Elgawhary, 1979; Lafever and Campbell, 1978; Polle, Konzak and Kittrick, 1978; Sapra et al., 1978; Lafever, Campbell and Foy, 1977; Mugwira and Patel, 1977; Moore, Kronstad and Metzger, 1976; Foy et al., 1965a, 1974; Mesdag and Slootmaker, 1969; and Fleming and Foy, 1968). Variation between this study and other reports in the literature indicates that screening for Al tolerance is imprecise. Such variation may have been due to factors like the extent of Al stress, screening techniques, composition of nutrient solutions, growth conditions, and seed source.

The daily patterns of change in nutrient solution pH induced by the cultivars (Fig. 3) were

TABLE 2. *Regression analyses between Al tolerance and pH of nutrient solutions induced by 20 winter cultivars of* T. aestivum

Independent variable	Dependent variable	Replicate	Regression coefficient	*Y*-Intercept	r^2	Level of significance
RTI	−Log mean H^+	1	0.163 ± 0.030	4.015 ± 0.016	0.609	0.0001
		2	0.186 ± 0.031	3.978 ± 0.016	0.673	0.0001
		3	0.249 ± 0.032	3.987 ± 0.017	0.772	0.0001
		1–3	0.204 ± 0.019	3.992 ± 0.010	0.656	0.0001
	Minimum pH	1	0.188 ± 0.060	3.758 ± 0.031	0.351	0.0059
		2	0.209 ± 0.045	3.696 ± 0.023	0.539	0.0002
		3	0.311 ± 0.054	3.685 ± 0.029	0.647	0.0001
		1–3	0.240 ± 0.032	3.712 ± 0.017	0.494	0.0001
	Slope of pH decline	1	0.031 ± 0.006	−0.068 ± 0.003	0.561	0.0001
		2	0.028 ± 0.005	−0.081 ± 0.002	0.674	0.0001
		3	0.034 ± 0.006	−0.085 ± 0.003	0.637	0.0001
		1–3	0.031 ± 0.005	−0.078 ± 0.002	0.436	0.0001
STI	−Log mean H^+	1	0.129 ± 0.105	3.990 ± 0.081	0.078	0.2340
		2	0.452 ± 0.144	3.724 ± 0.106	0.354	0.0056
		3	0.582 ± 0.087	3.638 ± 0.070	0.713	0.0001
		1–3	0.393 ± 0.066	3.781 ± 0.051	0.379	0.0001
	Minimum pH	1	0.129 ± 0.163	3.744 ± 0.126	0.033	0.4410
		2	0.562 ± 0.180	3.371 ± 0.133	0.350	0.0060
		3	0.720 ± 0.143	3.256 ± 0.115	0.586	0.0001
		1–3	0.464 ± 0.096	3.463 ± 0.074	0.287	0.0001
	Slope of pH decline	1	0.012 ± 0.021	−0.063 ± 0.017	0.018	0.5731
		2	0.073 ± 0.021	−0.124 ± 0.015	0.411	0.0023
		3	0.075 ± 0.170	−0.129 ± 0.014	0.523	0.0003
		1–3	0.047 ± 0.014	−0.100 ± 0.011	0.154	0.0019

similar to those reported previously (Fleming, 1983; Foy and Fleming, 1978, 1982; Mugwira et al., 1976; and Foy et al., 1965b). Fleming (1983) demonstrated that patterns of pH changes induced by *T. aestivum* in solution culture were determined by the source and relative supply of nitrogen in solutions. The period of pH decline was characterized by a rapid accumulation of NH_4^+ and the point of inflection for the reversal in pH change corresponded to depletion of NH_4^+ from nutrient solutions. Fleming (1983) also demonstrated that cultivar differences in NO_3^- and NH_4^+ uptake accounted for cultivar differences in daily pH profiles. Minor differences between this study and those reported by Fleming (1983), Foy and Fleming (1978, 1982), Mugwira et al. (1976), and Foy et al. (1965b) for the rate, direction, and magnitude of plant-induced pH changes may have reflected differences in the relative supply of NO_3^- and NH_4^+. Differences in cultivars tested and the initial pH of the nutrient solutions may also have affected patterns of pH change.

Regression analyses showed some variation between replicates (Table 2), and this resulted in lower explained variance in the regression analyses where the three replicates were combined. In each case, however, the RTI was significantly correlated with each of the pH variables (Table 2). Our analyses of climatic parameters in the growth room indicated some variation in air temperature, solution temperature, and relative humidity between replicates. Variation in climatic parameters and seedling vigor may have caused the variation in Al tolerance and plant-induced pH between replicates.

The significant correlations between the RTI (and STI) and the various pH variables demonstrated in this study are the first reported for a large number of cultivars. Mugwira and Elgawhary (1979) reported a correlation between Al tolerance and concentrations of Al in the roots of six cultivars of *T. aestivum* and also between root Al concentrations and plant-induced pH. However, results of regression analyses between Al tolerance and plant-induced pH were not presented. Our results are consistent with the hypothesis that plants resistant to acidification of the nutrient solution are exposed to a less Al-toxic rooting environment. Blamey, Edwards and Asher (1983) demonstrated that pH changes from 4.5 to 4.6 in dilute nutrient solutions resulted in a 26% decline in solution Al concentrations. Thus, the pH differences observed between the most Al-tolerant and Al-sensitive cultivars in this study (in the order of 0.35 pH units of Day 9) are clearly of biological relevance. It would be interesting to know whether the cultivars responded to

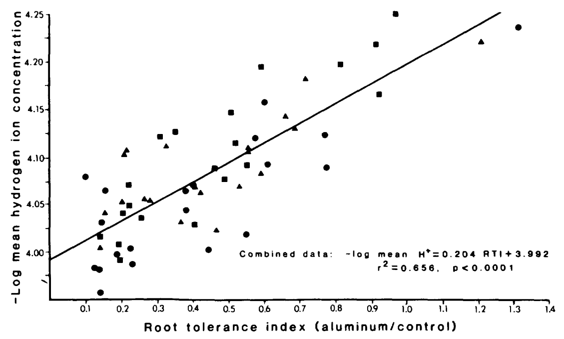

Fig. 4. Relationship between root tolerance index (RTI) and the negative log of the mean H^+ concentration induced in nutrient solutions by 20 winter cultivars of *T. aestivum*. Replicate 1 = triangles; Replicate 2 = circles; Replicate 3 = squares.

minimum pH (maximum Al concentration or acute Al stress) or mean H^+ concentration (cumulative exposure or chronic Al stress); however, the data do not support such conclusions.

The relationship between Al tolerance and plant-induced pH held for a broad range of Al tolerance. Solution pH accounted not only for the extremes in Al tolerance as demonstrated by Fleming (1983), Foy and Fleming (1978, 1982), Mugwira and Patel (1977), Mugwira et al. (1976), and Foy et al. (1965b, 1967), but also for the Al tolerance of intermediate cultivars. Furthermore, because the pH data were collected prior to the rapid rise in pH (presumably signaling depletion of NH_4^+), the data reflected characteristics of the growth solution at the time when differential Al tolerance was manifest. This is an improvement over the results of Foy and Fleming (1982), Mugwira and Elgawhary (1979), Mugwira et al. (1978), and Foy et al. (1967), where plant-induced pH values at the end of the experimental period (after the rapid rise in pH) were correlated with cultivar tolerance to Al. As discussed previously, correlations between Al tolerance and final solution pH may reflect the effects rather than the cause of differential Al tolerance.

This latter point is not entirely satisfactory. Inhibition of root elongation in *Vigna unguiculata* (cowpea), *Allium cepa* (onion), and *T. aestivum* occurs over a period of 6–18 hr (Horst, Wagner and Marschner, 1983; Morimura, Takahashi and Matsumoto, 1978; Henning, 1975; Clarkson, 1965). In this study, plants supplied with 74 μM (2.0 mg L^{-1}) Al for 3–5 days showed visual symptoms of Al toxicity that were reflected in the subsequent Al tolerance ratings. Thus, differences in pH must be generated over a period of days, if not hours, if they are to account for cultivar differences in Al tolerance. The screening technique utilized in this investigation was not sufficiently sensitive to identify short-term differences in pH between cultivars. We are currently addressing this issue using an alternative technique.

The data presented here have demonstrated a correlation between pH's of nutrient solutions induced by 20 cultivars of *T. aestivum* and cultivar tolerance to Al. These data are consistent with the hypothesis that plants resistant to acidification of the nutrient solution and maintaining a relatively high pH can reduce the solubility and, hence, toxicity of Al. However, further studies are required to elucidate the role of cultivar differences in plant-induced pH in determining cultivar tolerance to Al.

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