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Kinetics of Aluminum Uptake by Excised Roots of Aluminum-Tolerant and Aluminum-Sensitive Cultivars of *Triticum aestivum* L.[1]

Guichang Zhang* and Gregory J. Taylor

Department of Botany, University of Alberta, Edmonton, Alberta, T6G 2E9, Canada

ABSTRACT

Uptake of aluminum (Al) by excised roots of two Al-tolerant cultivars and two Al-sensitive cultivars of *Triticum aestivum* L. (wheat) was biphasic, with a rapid phase of uptake in the first 30 minutes followed by a linear phase of uptake up to 180 minutes. At the end of the uptake period, higher concentrations of Al were found in roots of the Al-sensitive cultivars (Neepawa and Scout-66) than in the Al-tolerant cultivars (Atlas-66 and PT-741), but differences were small. Experiments testing the effectiveness of several desorption agents demonstrated that citric acid was most effective in desorption of loosely bound Al (the putative apoplasmic compartment) followed by others in the order tartaric acid > EDTA > $CaSO_4$ = $ScCl_3$. In all cultivars, 30 minutes of desorption with citric acid depleted the rapidly exchanging, putative apoplasmic compartment, although some tightly bound Al remained in that compartment. The relationship between Al remaining after desorption and time in the uptake medium was nearly linear and no distinction was observed between Al-tolerant and Al-sensitive cultivars. However, uptake of Al by the Al-tolerant cultivars was increased by treatment with the protonophore 2,4-dinitrophenol (DNP), while uptake of Al by Al-sensitive cultivars was relatively unaffected. Such results suggest the possible involvement of an active exclusion mechanism in Al-tolerant cultivars of *T. aestivum*.

Plants may tolerate potentially phytotoxic concentrations of Al in the growth substrate by two basic strategies (13, 15, 16, 18). An effective strategy would be to limit entry of Al into the symplasm where it may exert its primary toxic effect (exclusion mechanisms). If exclusion were incomplete or ineffective, tolerance might be achieved by detoxification or compartmentation of Al in the cytosol (internal tolerance mechanisms) (16). While many authors have denied the existence of exclusion mechanisms (4, 13), Taylor suggested that exclusion could be achieved by means of a pH barrier at the rhizosphere, selective permeability of plasma membrane, exudation of chelates or immobilization of Al in the cell wall (16).

The proposed mechanisms of exclusion have received experimental support. For example, Taylor and Foy (21–23), and Fleming (3) demonstrated a correlation between the Al tolerance of cultivars of *Triticum aestivum* and their ability to resist acidification of the rhizosphere, but differences in plant-induced pH do not appear to be the primary cause of different tolerance to Al in these species (19, 20). In other studies, selective permeability of the plasma membrane to Al was suggested by increased uptake of Al by roots of several species under nonmetabolic conditions (5, 24). Ojima *et al.* (11) and Ojima and Ohira (12) found that Al-tolerant cell cultures of *Daucus carota* exuded more citrate into the growth medium than Al-sensitive cultures, and addition of malic or citric acid to Al-sensitive cultures mitigated the toxic effects of Al. Finally, Clarkson (2) found that 85 to 90% of the total Al accumulated by roots of *Hordeum vulgare* was tightly bound to cell wall material and suggested that the Al was bound to free carboxyl groups of polygalacturonic acids in the middle lamella.

Nonetheless, experimental support for exclusion is incomplete. Few studies have differentiated between uptake of Al into apoplasmic and symplasmic compartments (16). This information is essential for interpretation of experimental results and identification of Al tolerance mechanisms. Several authors have attempted to characterize Al uptake by comparing kinetics of uptake by different species at high concentrations of Al in the growth solution (either 1.0 or 1.13 mM) (5, 14, 25). While such experiments do provide information on Al uptake in the apoplasmic and symplasmic compartments, comparison of plants with such diverse genetic background using such high concentrations of Al make conclusions about tolerance mechanisms speculative.

In the present study, the kinetics of Al uptake by excised roots of Al-tolerant and Al-sensitive cultivars of *T. aestivum* were investigated. Use of graphite furnace atomic absorption spectrophotometry permitted uptake experiments to be performed using a physiologically relevant concentration of Al (75 μM). The results reported demonstrate uptake of Al into two distinct compartments, and suggest the involvement of an active exclusion mechanism in Al-tolerant cultivars of *T. aestivum*.

MATERIALS AND METHODS

Preparation of Plant Material

Seeds of two Al-tolerant cultivars (Atlas-66 and PT-741) and two Al-sensitive cultivars (Neepawa and Scout-66) of *Triticum aestivum* L. (wheat) were surface sterilized in 1.2%

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sodium hypochlorite for 20 min, and germinated overnight in a solution of 0.005 g/L Vitavax to prevent fungal growth. Seedlings were grown for 7 d on nylon mesh suspended over 16 L of nutrient solution containing (mM) 3.30 NO_3^--N, 0.30 NH_4^+-N, 0.10 P, 0.80 K, 1.00 Ca, 0.30 Mg, 0.10 S; and (μM) 34 Cl, 60 Na, 10 Fe, 6 B, 2 Mn, 0.15 Cu, 0.5 Zn, and 0.10 Mo (pH 4.5) in a growth chamber with 16 h of light (20°C, 68% RH) and 8 h of darkness (16°C, 85% RH). After 5 d of growth, plants were transferred to fresh nutrient solutions.

Uptake of Al

Thirty excised root tips (2.0 cm) were placed in each of 50 'absorption tubes.' Absorption tubes consisted of open-ended Plexiglas tubes (12 cm length, 2.2 cm diameter), with a nylon mesh barrier located 1.5 cm from the bottom. Four holes were cut in the tubes beneath the mesh barrier to permit circulation of absorption solution inside and outside of the tubes. During excision of roots, absorption tubes containing excised roots were placed in an aerated nutrient solution. When excision was complete (within 60 min), the tubes were transferred to an aerated solution of 1.0 mM $CaSO_4$ for 30 min. Uptake experiments were initiated by transferring the absorption tubes containing roots to 80 mL glass jars containing 50 mL of an aerated solution of 1.0 mM $CaSO_4$ and 75 μM Al (pH 4.5). Absorption tubes were covered at the top with nylon mesh, and the jars were incubated in a water bath at 23°C. Five replicate tubes were removed from the absorption solutions after 0, 5, 10, 15, 20, 30, 60, 90, 120, 150, and 180 min of uptake. Roots were rinsed briefly with 1 mM $CaSO_4$ and then with deionized water (300 mL per tube), and prepared for determination of Al by graphite furnace atomic absorption spectrophotometry.

Screening of Desorption Agents

Using an Al-sensitive cultivar, Neepawa, this experiment was designed to select a desorption agent which effectively removed Al from the apoplasm. After uptake of Al for 2 h as described above, absorption tubes with roots were removed from absorption solutions, rinsed with cold deionized water (4°C), and transferred to jars with 50 mL aerated desorption solution. Desorption agents included two multivalent cations, Ca^{2+} ($CaSO_4$) and Sc^{3+} ($ScCl_3$) and three effective chelators of Al, EDTA, tartaric acid, and citric acid. Desorption agents were supplied at 0.5 mM, a concentration providing roughly 75 times more desorption agent than total Al absorbed by the roots at the end of uptake period. Desorption solutions were set to pH 4.5 and maintained at 0°C in an ice water bath to minimize loss of Al from the symplasm. After 0, 5, 10, 15, 20, 30, 60, 90, 120, and 180 min of desorption, 5 replicate absorption tubes were removed from desorption solutions, rinsed with deionized water, and prepared for determination of Al.

Determination of Desorption Time

This experiment was designed to determine if patterns of desorption with time varied between cultivars. After uptake of Al for 2 h, roots from Atlas-66, Neepawa, PT-741, and Scout-66 were removed from absorption solution, rinsed with cold deionized water (4°C) and transferred to 0.5 mM citric acid (pH 4.5) at 0°C for different time periods (0, 5, 10, 15, 20, 30, 60, 90, 120, 180 min). At the end of each desorption period, roots were rinsed and prepared for determination of Al.

Determination of Slowly Exchangeable Al

After uptake at 23°C for 0, 5, 10, 15, 20, 30, 60, 90, 120, 150, and 180 min, absorption tubes with roots were removed from absorption solutions, rinsed with cold deionized water (4°C), and transferred to 0.5 mM citric acid at 0°C for 30 min to remove readily exchangeable Al from the apoplasm. At the end of desorption, roots were rinsed with deionized water, and prepared for determination of Al.

Inhibitor Studies

Excised roots were placed in absorption solutions (75 μM Al and 1 mM $CaSO_4$) with and without 0.1 mM DNP. After 0, 15, 30, 60, 120, and 180 min of uptake, roots were removed from absorption solutions, rinsed with cold deionized water (4°C), and transferred to 0.5 mM citric acid at 0°C for 30 min to remove Al from the apoplasm. At the end of the desorption period, roots were removed, rinsed with dionized water, and prepared for determination of Al.

Determination of Al

Root samples were air-dried for 12 h at room temperature, dried to constant weight at 55°C, weighed, transferred to 50 mL borosilicate tubes, and ashed at 500°C for 24 h. The resulting ash was dissolved in 200 μL concentrated HNO_3, oxidized with 200 μL 50% H_2O_2, and diluted to 40 mL with deionized water. Aluminum concentrations were analyzed on a Perkin-Elmer 3030 atomic absorption spectrophotometer with an HGA-500 graphite furnace attachment. Twenty μL of diluted sample (0.6 mL sample:1.2 mL deionized water) were mixed with 20 μL $Mg(NO_3)_2$ as a matrix modifier, dried at 150°C for 45 s, pretreated at 1700°C for 45 s, and atomized at 2500°C for 5.5 s on a L'vov platform in a pyrolytically coated graphite tube. Concentrations were calculated by integration of peak area, and expressed as micrograms Al per gram dry weight (μg Al g^{-1}). For preparation of samples and standards for graphite furnace atomic absorption spectrophotometry, deionized water (>18 megohm/cm) and high purity reagents were used. Except for the ashing procedures, samples and standards were prepared and stored in polyethylene containers prewashed with dilute HNO_3 and deionized water.

RESULTS

Uptake of Al by Al-tolerant and Al-sensitive cultivars showed to phases, a rapid phase in the first 30 min followed by a linear phase up to 180 min (Fig. 1). In the first phase, differences between Al-tolerant and Al-sensitive cultivars were small, but concentrations of Al were higher in the Al-sensitive cultivars Neepawa and Scout-66, than in the Al-tolerant cultivars Atlas-66 and PT-741 after 30 min of uptake. In the

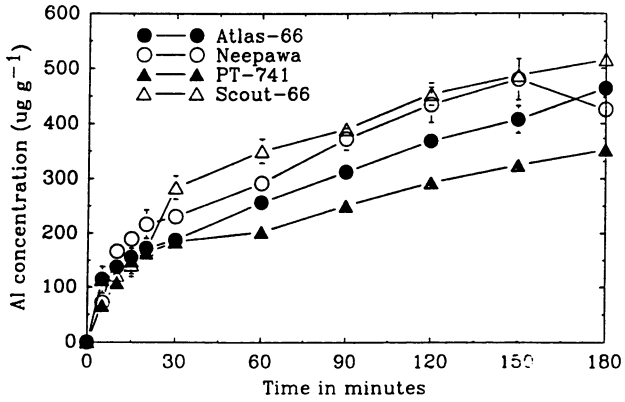

Figure 1. Uptake of Al by excised roots of Al-tolerant and Al-sensitive cultivars of *T. aestivum*. Absorption solutions contained 75 μM Al and 1 mM $CaSO_4$ at pH 4.5 and 23°C.

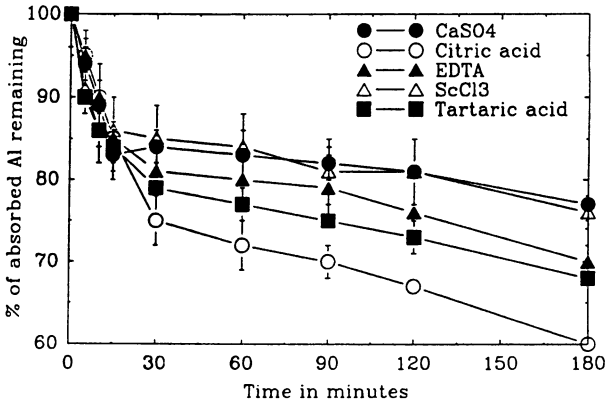

Figure 2. Desorption of Al from excised roots of an Al-sensitive cultivar of *T. aestivum*, Neepawa. Uptake for 2 h in 75 μM Al and 1 mM $CaSO_4$ at pH 4.5 and 23°C, was followed by desorption in 0.5 mM $CaSO_4$, $ScCl_3$, EDTA, citric acid, or tartaric acid at 0°C.

linear phase, little difference was observed in the rate of Al uptake between Al-tolerant cultivars (1.79 ± 0.12 μg Al g^{-1} min^{-1}, Atlas-66; 1.18 ± 0.11 μg Al g^{-1} min^{-1}, PT-741) and Al-sensitive cultivars (2.18 ± 0.25 μg Al g^{-1} min^{-1}, Neepawa; 1.55 ± 0.24 μg Al g^{-1} min^{-1}, Scout-66), thus concentrations of Al remained higher in roots of the Al-sensitive cultivars (with the exception of an anomalous point at 180 minutes for Neepawa) (Fig. 1).

Dual kinetics similar to the pattern of Al uptake reported here have commonly been interpreted as representing uptake into the apoplasm (rapid phase) and uptake across the plasma membrane (linear phase). Thus, in a second experiment, an Al-sensitive cultivar (Neepawa) was used to test the effectiveness of various desorption agents for removal of Al from the putative apoplasmic compartment. As expected, desorption occurred in two phases, a rapid phase in the first 30 min followed by a linear phase up to 180 min. During the first phase, citric acid was most effective in desorbing Al, followed by others in the order tartaric acid > EDTA > $CaSO_4$ = $ScCl_3$. By 30 min, 25 ± 3% of absorbed Al was removed by treatment with citric acid, while 21 ± 1, 19 ± 1, 16 ± 2, and 15 ± 4% of absorbed Al were removed by tartaric acid, EDTA, $CaSO_4$ and $ScCl_3$, respectively. After removal of this rapidly exchangeable Al, the rate of desorption with time was relatively unaffected by the desorption agents used (0.99 ± 0.01, 0.07 ± 0.01, 0.08 ± 0.02, 0.06 ± 0.03, and 0.04 ± 0.02 μg Al g^{-1} min^{-1} for citric acid, tartaric acid, EDTA, $CaSO_4$ and $ScCl_3$ respectively, see Fig. 2). Thus, 30 min of desorption with citric acid appeared most effective for removal of Al from the putative apoplastic compartment (readily exchangeable Al). With this treatment, all four cultivars showed a similar pattern of Al desorption; no difference was observed in the rate of desorption during the linear phase between Al-tolerant cultivars (0.06 ± 0.02 μg Al g^{-1} min^{-1}, Atlas-66; 0.10 ± 0.01 μg Al g^{-1} min^{-1}, PT-741) and Al-sensitive cultivars (0.10 ± 0.02 μg Al g^{-1} min^{-1}, Neepawa; 0.06 ± 0.02 μg Al g^{-1} min^{-1}, Scout-66) (Fig. 3).

Uptake of Al into the slowly exchangeable fraction was observed by monitoring Al remaining in roots after a period of uptake (0–180 min) followed by 30 min desorption in citric acid. For each cultivar, the rate of uptake was nearly linear.

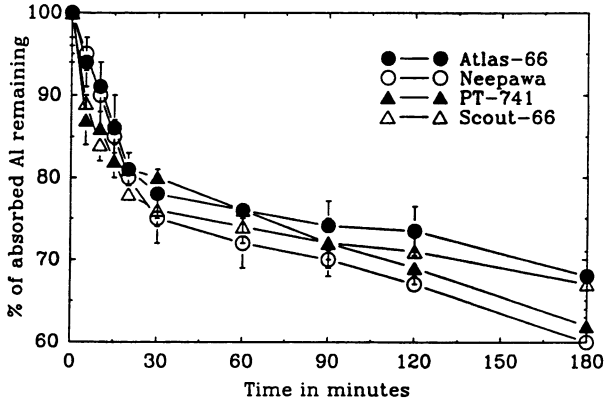

Figure 3. Desorption of Al from excised roots of Al-tolerant and Al-sensitive cultivars of *T. aestivum*. Uptake for 2 h in 75 μM Al and 1 mM $CaSO_4$ at pH 4.5 and 23°C, was followed by desorption in 0.5 mM citric acid at 0°C.

Deviation from linearity occurred primarily during the first 30 minutes of uptake, suggesting that the desorption treatment was not completely effective in removal of Al from the putative apoplasmic compartment. Incomplete desorption of the putative apoplasmic compartment was also suggested by the fact that extrapolation of the linear phase of absorption to time zero (Fig. 1) gave a greater estimate of the size of the apoplasmic compartment than extrapolation of the linear phase of desorption to time zero (Fig. 3; Table I). Nevertheless, the desorption technique was largely effective in isolating the linear phase of uptake. In this phase, the rate of uptake varied between cultivars; however, no distinctive pattern of uptake distinguishing Al-tolerant from Al-sensitive cultivars was observed (2.24 ± 0.11, 1.55 ± 0.07, 2.20 ± 0.05, 1.51 ± 0.07 μg Al g^{-1} min^{-1} for Atlas-66, PT-741, Neepawa, and Scout-66, respectively; see Fig. 4).

In the Al-sensitive cultivars, the linear phase of Al uptake was relatively insensitive to treatment with the protonophore DNP. In the Al-sensitive cultivar, Neepawa, the rate of Al uptake was increased 7.0% by treatment with DNP (Fig. 5A). In Scout-66, a 24.7% increase was observed (Fig. 5B). In

Table I. *Estimated Contribution of the Rapidly Exchanging Apoplasmic Compartment to Total Uptake of Al in Al-Tolerant and Al-Sensitive Cultivars of T. aestivum*

Values were calculated by extrapolation of the linear phase of Al uptake and the linear phase of Al desorption to time zero, and are expressed as a percent of total Al uptake.

Estimated by:	Al-Tolerance Cultivars		Al-Sensitive Cultivars	
	Atlas-66	PT-741	Neepawa	Scout-66
Linear phase of uptake	31	40	31	46
Linear phase of desorption	20	17	22	23

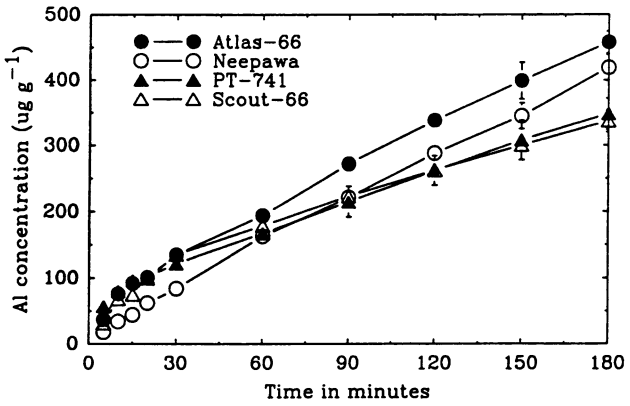

Figure 4. Uptake of Al into the slowly exchangeable fraction of excised roots of Al-tolerant and Al-sensitive cultivars of *T. aestivum*. Uptake in 75 μM Al and 1 mM $CaSO_4$ at pH 4.5 and 23°C, was followed by desorption in 0.5 mM citric acid at pH 4.5 and 0°C for 30 min.

contrast, the rate of Al uptake by the Al-tolerant cultivars was strongly increased by DNP, with Atlas-66 showing a 51.9% increase and PT-741 a 73.1% increase (Fig. 5, C and D). Similar effects of DNP on uptake of Al in Al-tolerant and Al-sensitive cultivars were also observed with an alternative experimental design in which all four cultivars were tested simultaneously and rates of uptake (with and without DNP) were determined by sampling after 30 and 120 min of absorption.

DISCUSSION

To our knowledge, this is the first report comparing kinetics of Al uptake between Al-tolerant and Al-sensitive cultivars of the same species. In both Al-tolerant and Al-sensitive cultivars, uptake of Al by excised roots was biphasic. Although the identity of these two phases has not been investigated here, such kinetics have been commonly interpreted as representing uptake into the apoplasm (rapid phase) and uptake across plasma membrane (the linear phase) (8). If this designation is correct, uptake of Al in the apoplasm was rapid and saturated within 30 min (Fig. 1). A similar rapid phase of uptake was observed in experiments with *Brassica oleracea*, *Lactuca sativum*, *Pennisetum clandestinium*, although saturation was not complete until 60 min of uptake (5). In *Pinus taeda* and *Gleditsia triacanthus*, saturation was complete in 4 h (14). Such differences between experiments may reflect differences between species, or differences in experimental conditions such as pH, Al concentration, and temperature of absorption solutions. In our experiments, the concentration of Al in absorption solutions was 75 μM, a concentration which does not affect growth of Al-tolerant cultivars of *T. aestivum*, but seriously reduces growth of Al-sensitive cultivars (21, 22, 28). In contrast, the experiments of Huett and Menary (5) and Wagatsuma (25) used 1.0 and 1.13 mM Al, respectively.

At the end of the first phase of uptake, roots of the Al-sensitive cultivars (Neepawa and Scout-66) showed higher concentrations of Al than roots of the Al-tolerant cultivars (Atlas-66 and PT-741) (Fig. 1). These differences may reflect a lower cation exchange capacity of the cell wall material in the Al-tolerant cultivars (7, 10), which might contribute to Al

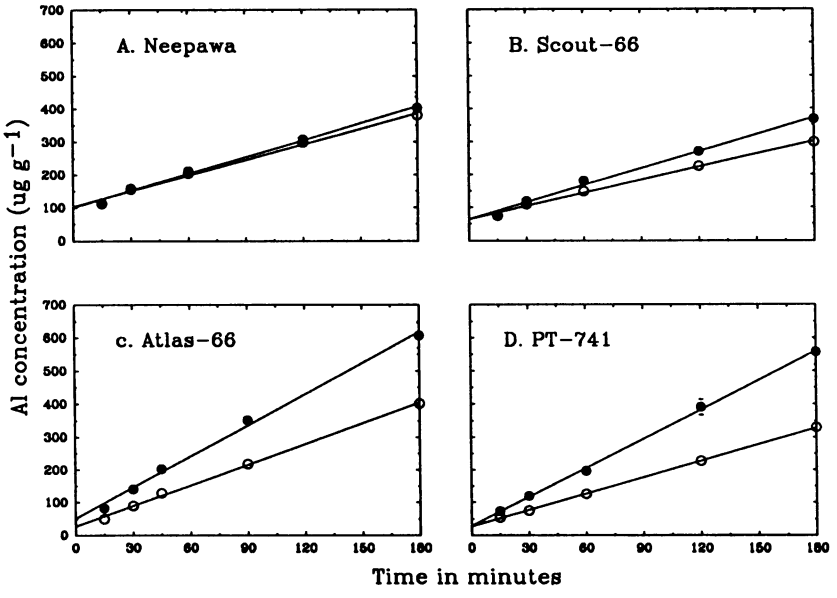

Figure 5. Uptake of Al by excised roots of Al-tolerant and Al-sensitive cultivars of *T. aestivum*; A, cv Neepawa; B, cv Scout-66; C, cv Atlas-66; D, cv PT-741. Uptake in 75 μM Al and 1 mM $CaSO_4$ (pH 4.5, 23°C), with (●) and without (○) 0.1 mM DNP, was followed by desorption in 0.5 mM citric acid at pH 4.5 and 0°C for 30 min.

tolerance by altering membrane selectivity and nutrient absorption (16, 17). Extrapolation of the linear phase to time zero indicated that less than 50% of absorbed Al was localized in the putative apoplasmic compartment in each of the four cultivars (Table I), a value well below the 75 to 95% reported to be associated with cell wall material in roots of *Hordeum vulgare*, *B. oleracea*, *L. sativum*, and *P. clandestinium* (2, 5). While such differences may result from variation of properties of cell wall material and characteristics of metabolism between different species, it is also possible that the linear phase of uptake included both symplasmic and apoplasmic accumulation of Al. Precipitation of Al phosphate compounds or formation of insoluble polynuclear Al species could account for immobilization of Al in the apoplasm during the linear phase of uptake. If accumulation of Al in the apoplasm occurs during the linear phase, then extrapolation of the linear phase to time zero may underestimate apoplastic uptake.

Although the four cultivars showed similar rates of Al uptake during the linear phase, we decided to investigate this phase of uptake using experiments designed to remove readily exchangeable Al from the apoplasm. Of various desorption agents tested, citric acid was most effective in desorption of Al from the putative apoplasmic compartment. The effectiveness of citrate was consistent with its ability to protect plant cells from Al injury (4, 27); citric acid is a tridentate chelate with chelation through two terminaol carboxyl groups and a central hydroxyl group (6), resulting in a high-stability constant (about 10^8) for 1:1 Al-citrate chelates (9). Aluminum-EDTA and Al-tartaric acid complexes are less stable, possibly accounting for the less effective nature of these desorption agents. The relative inability of Ca^{2+} and Sc^{3+} to desorb Al from the putative apoplasmic compartment was surprising, and suggests that Al uptake and desorption from the apoplasm may not be solely in ion exchange phenomenon. Thirty min desorption in citric acid appeared sufficient for completion of the rapid desorption phase (Fig. 2). The biphasic pattern of desorption of Al from all four cultivars (Fig. 3) was similar to desorption of Al from roots of *B. oleracea*, *L. sativum*, and *P. clandestinium* (5).

While desorption with citric acid was largely effective in isolating the linear phase of uptake, uptake of Al into this slowly exchangeable fraction deviated from linearity during the first 30 min of uptake (Figs. 4 and 5), and extrapolation of uptake to time zero indicated some Al remained in the apoplasm of all four cultivars (Fig. 4). Differences in the estimated size of the apoplasmic compartment based upon extrapolation of the linear phase of uptake and the linear phase of desorption also suggested incomplete desorption of Al from the apoplasm (Table I). Incomplete desorption of the apoplasm has been reported in other kinetic studies. For example, a small fraction of nonexchangeable ^{63}Ni in cell walls of *H. vulgare* and ^{109}Cd in cell walls of *Glycine max* was reported in experiments using 1 mM EDTA (8) and 0.5 mM $CaCl_2$ or 0.4 to 10 μM $CdCl_2$ (1) as desorption agents, respectively.

If the rapid and linear phases of Al uptake reported in this study reflect uptake into the apoplasmic and symplasmic compartments, respectively, then the pattern of uptake into the slowly exchangeable fraction was inconsistent with the operation of an exclusion mechanism in Al-tolerant cultivars. If exclusion were important, different rates of uptake should have distinguished Al-tolerant from Al-sensitive cultivars. This was not observed. We have, however, questioned the identity of the linear phase of uptake. This phase may include progressive accumulation of tightly bound Al in both the apoplasm and symplasm. Thus, the failure to detect differences between tolerant and sensitive cultivars in the rate of uptake across the plasma membrane (one component of the linear phase) may have been due to differences in the rate of accumulation of tightly bound Al in the apoplasm (the remaining component of the linear phase). This interpretation is consistent with Wagatsuma and Ezoe's (26) suggestion that plants that effectively exclude Al at the plasma membrane may promote polymerization and accumulation of hydroxy Al in the apoplasm, thus contributing to detoxification of Al. Further investigation of the cellular localization of Al in the two phases of uptake will be needed to clarify this question.

While Haug and Caldwell (4), and Roy *et al.* (13) suggested that exclusion mechanisms are not important in Al tolerance, the potential operation of an exclusion mechanism in Al-tolerant cultivars of *T. aestivum* was suggested in this study by uptake experiments using the protonophore DNP. Increased rates of uptake of Al by roots of Al-tolerant cultivars treated with DNP (Table II) suggested that metabolic exclusion of Al from the symplasm of Al-tolerant cultivars occurred under normal aerobic conditions (without respiratory inhibitor). In contrast, the minimal effect of DNP on uptake by Al-sensitive cultivars suggests that uptake and accumulation of Al is not as closely regulated in a direct energy-dependent fashion (Table II). Increased uptake of Al in roots treated with DNP was also reported in experiments with several species by Huett and Menary, who suggested that DNP increased permeability of the plasma membrane to Al (5).

Since DNP is reported to uncouple oxidative phosphorylation, impair membrane structure and permeability, and destroy the proton gradient across the plasma membrane, the way which DNP affected uptake of Al in Al-tolerant and Al-sensitive cultivars cannot be identified. However, metabolic exclusion of Al might be achieved by means of an active efflux of Al into the apoplasm, by metabolic maintenance of plasma membrane structure and function in the face of Al stress (repair), or by enhanced exudation of Al chelators such as citric acid and tartaric acid in the cell wall space of Al-tolerant cultivars. Characteristics of the effects of other met-

Table II. *Rate of Al Uptake (μg Al g^{-1} min^{-1}) by Al-Tolerant and Al-Sensitive Cultivars of T. aestivum from Absorption Solutions With and Without 0.1 mM DNP*

Treatment	Al-Tolerant Cultivars		Al-Sensitive Cultivars	
	Atlas-66	PT-741	Neepawa	Scout-66
Control	2.06 ± 0.08	1.75 ± 0.08	1.86 ± 0.12	1.50 ± 0.08
+ DNP	3.13 ± 0.13	3.03 ± 0.11	1.99 ± 0.14	1.87 ± 0.09
% Increase	51.9*	73.1*	7.0	24.7*

* Indicates a significant increase in the rate of Al uptake from solutions with DNP compared to uptake from control solutions ($P < 0.05$).

abolic inhibitors on kinetics of Al uptake and more definitive information on the localization of Al during the linear phase of uptake may help to identify possible exclusion mechanisms.

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