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ORIGINAL ARTICLE

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Root growth enhancement by rhizospheric aluminum treatment in *Quercus serrata* Thunb. seedlings

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Abstract This article discusses the effect of aluminum on root growth of *Querucus serrata* Thunb. In a 9-week hydroponics experiment, the effects of various concentrations (0 to 5.0 mM) of Al on root growth were examined. Results revealed that root biomass increases with the increase in Al concentration up to 2.5 mM, and then it tended to decrease. In the next experiment, the effects of H^+ and Al^{3+} on roots were compared in a 4-week hydroponics experiment using three treatment solutions: control (pH 6.0), −Al (without Al, pH 3.5), and +Al (with 2.5 mM Al, pH 3.5). No clear difference in the biomass and root length between the control and −Al treated roots was observed, and root and shoot biomass were increased by Al treatment. These results confirmed that the H^+ concentration level, at a pH of 3.5, is not toxic for *Q. serrata* and the Al-induced increase in root biomass is not caused by the amelioration of H^+ toxicity by Al. In the third experiment, roots were exposed to an Al solution (pH 3.6) intermittently. This treatment clarified that Al stimulated rooting and root elongation. In the fourth experiment, the effect of 1 mM Al on root growth during a 15-month period in a sand culture were examined. This experiment confirmed that Al stimulated good growth and development of root systems at appropriate concentrations. Therefore, it is considered that Al-induced root growth enhancement occurs as a long-term and short-term phenomenon.

Key words Aluminum effect · Rooting · Root elongation· *Querucus serrata* Thunb.

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Introduction

In Japan, most of the forest soil is acidic, and the pH of forest soils ranges from 4.0 to 6.0 (Kawada 1989). Takahashi et al. (2001) reported that the average pH of forest soil solution in Japan is approximately 5.1 and most of the soil has potentially high amounts of exchangeable aluminum (Al), which is known to be toxic to many plant species. Exchangeable Al increases when the pH of soil solution falls below 5.0 and increases dramatically when the pH is less than 4.5. The rhizosphere soil pH around the roots is lower than that of the bulk soil, including the subsoil, due to the release of H^+ and organic anions from the roots accompanied by the uptake of cations, thereby making the concentrations of exchangeable Al around the roots higher than the average bulk soil value (Gobran and Clegg 1996; Göttlein et al. 1999; Smith and Pooley 1989; Ohno 1989). Therefore, tree roots in the forests in Japan are thought to be exposed to relatively high concentrations of Al^{3+}.

The effects of Al on plants and the mechanisms of Al toxicity have been studied for many years, and it is well known that Al inhibits root growth in many plant species. On the other hand, it is also known that woody plant species are relatively more tolerant to Al than agricultural crop species (Keltjens and Loenen 1989; McCormick and Steiner 1978; Ryan et al. 1986). Some reports revealed that the root biomass of tree species increases after treatment with Al (Thornton et al. 1986b, 1989), and in most of these reports, the proposed mechanism driving the increase in root biomass is the amelioration of H^+ toxicity by polyvalent cations such as Al^{3+}. The mechanism of amelioration of H^+ toxicity by Al was demonstrated at a pH of about 4.0 using cultivated plants, such as wheat, cucumber, Japanese radish, pea, etc., however, the optimum pH for growth of these plant species is around 6.0 (Kinraide 1993; Wagatsuma and Kaneko 1987). It has been unclear whether this mechanism applies to tree species growing in more acidic soils. Therefore, it is necessary to confirm whether growth stimulation by Al in tree species is related to the alleviation of H^+

toxicity or whether Al plays some role in stimulating root growth.

This study examines whether Al can promote the growth of *Quercus serrata* Thunb., which is a typical temperate forest species in Japan and exhibits a tendency of enhanced root growth with increasing Al concentrations (Tomioka and Takenaka 2001). In the first experiment, the effects of various Al concentrations on root growth were examined and the optimal Al concentration for the growth of *Q. serrata* was established. In the second experiment, the effects of Al on growth and root elongation were confirmed by comparing the effects of H^+ and Al^{3+}; it was also confirmed that the growth enhancement was not an amelioration effect of H^+ toxicity induced by Al^{3+}. In the third experiment, intermittent Al treatments were used to assess whether temporary exposure to Al affects growth in the same manner as continuous treatments. In the fourth experiment, the long-term stimulatory effects of Al on root growth were assessed.

Materials and methods

Effect of various Al concentrations on growth (experiment 1)

One-year-old *Quercus serrata* Thunb. seedlings were collected from a secondary forest on the campus of Nagoya University, Aichi, Japan. The roots of the seedlings were rinsed well under running water before transplantation into 300-mL plastic pots. The seedlings were grown hydroponically in modified 1/5 Hoagland's No. 2 (hereafter referred to as nutrient solution), containing 1.2 mM KNO_3, 0.8 mM $Ca(NO_3)_2{\cdot}4H_2O$, 0.4 mM $MgSO_4{\cdot}7H_2O$, 0.2 mM $NH_4H_2PO_4$, 91 μM·$MnCl_2{\cdot}4H_2O$, 17.9 μM·$FeCl_3{\cdot}6H_2O$, 0.8 μM $ZnSO_4{\cdot}7H_2O$, 0.3 μM $CuSO_4{\cdot}5H_2O$, 4.6 μM H_3BO_3, and 0.5 μM $NaMoO_4{\cdot}2H_2O$, in a phytotron at 27°C and 70% relative humidity, in a photoperiod of 12 h/12 h (day/night), and with irradiation of 150 μmol $m^{-2}s^{-1}$ for 2 weeks. After growth for 2 weeks, seven pots of seedlings were cultured using each of the seven treatments prepared with 0, 0.1, 0.25, 0.5, 1.0, 2.5, or 5.0 mM $AlCl_3{\cdot}6H_2O$, respectively, for 9 weeks. The Al^{3+} activities in treatments one to seven were calculated as 0, 0.05, 0.13, 0.29, 0.68, 2.00, and 4.43 mM, respectively, using GEOCHEM-PC (Parker et al. 1995). The solution was changed every 2 weeks, and the pH of the solution was adjusted to 3.5 ± 0.1 to prevent Al precipitation and was readjusted every 2 days with 1 N HCl. After exposure to the treatment solutions for 9 weeks, the seedlings were harvested and oven-dried at 80°C for 48 h to determine the root and shoot dry weights.

Effects of H^+ and Al^{3+}on growth (experiment 2)

Two-year-old *Q. serrata* seedlings were purchased from Takemoto-en, Tottori, Japan. Their roots were rinsed well with running water before being transplanted, two seedlings per pot, into five plastic 1-liter pots. The seedlings were grown hydroponically in a phytotron for 1 month with the nutrient solution. Three treatment solutions, namely, control, low pH (–Al), and 2.5 mM Al (+Al) were prepared. The pH of the treatment solution was adjusted with 1 N HCl and 1 N NaOH. The Al treatment solution was prepared by adding $AlCl_3{\cdot}6H_2O$ to the nutrient solution. In each treatment, five seedling pots were cultured for 4 weeks with weekly renewals of the solution. In the case of the –Al and +Al treatments, the pH of the treatment solution was readjusted to 3.5 ± 0.1 every 2 days. The pH of the control solution increased to approximately 7.0 during the first 24 h, and following the renewal of the solution, the pH was maintained at a constant value for the remainder of the experiment.

After 4 weeks, the seedlings were harvested and the roots were rinsed five times with distilled water. The dry weight of the seedlings was then determined and the lengths of five newly grown roots, which emerged after the treatment was initiated, were measured for each seedling using LIA32 software (Yamamoto 2000). Ten replications of the experiment were performed.

Effect of intermittent Al treatment on root elongation and rooting (experiment 3)

One-year-old *Q. serrata* seedlings were purchased from Takemoto-en. The roots of the seedlings were washed in running water and the seedlings were grown hydroponically in the nutrient solution (pH 5.0) for 1 month in a phytotoron. The treatment was provided intermittently as follows: roots were exposed for 1 h per day to 2.5 mM $AlCl_3$ solution or distilled water, the pH of which was adjusted to 3.6 with 1 N NaOH and 1 N HCl. For the remaining 23 h, the roots were exposed to the nutrient solution (pH 5.0). Before and after the 1-h treatment, the roots were washed twice with distilled water. During the course of the experiment (50 days), the nutrient solution was changed once a week. After treatment, the morphology of the roots was observed and the lengths of the newly grown roots were measured as described earlier. The oven-dried roots were used for the analysis of nutrient status.

Effect of long-term Al effect on growth (experiment 4)

Two-year-old *Q. serrata* seedlings were purchased from Takemoto-en. The roots were washed well with running water before they were transplanted, three seedlings per pot, in 5.1-l plastic pots with siliceous sand (Tokai-M No. 3). Five pots were placed in a 35-l plastic box on January 27, 2002. The seedlings were given the complete nutrient solution without Fe twice a week and 39 μM $FeCl_3{\cdot}6H_2O$ solution once every 2 weeks. After growth for 2 months, the seedlings were exposed to each of the three treatment solutions shown in Table 1 [control, low pH (–Al), and 1.0 mM Al (+Al)] and prepared as described earlier. The pH of the solution was adjusted with 1 N HCl and 1 N NaOH to 5.0 for the control and 3.5 for –Al and +Al. During the treatment, approximately 201 of treatment solution was poured into

the 35-l plastic box, which was subsequently decanted after approximately 1 h. Throughout the 15-month experiment period, the 1-h treatment was performed twice a week and the Fe solution described earlier was provided once every 2 weeks. After the 15-month treatment period, shoot height was measured and the roots were gently washed several times with distilled water, after which three secondary roots were randomly collected in each seedling. The number of tertiary roots was counted and the lengths of the secondary and tertiary roots were measured as described earlier. After oven-drying the roots as described earlier, shoot and root dry weights were measured. The oven-dried roots were used for the analysis of nutrient status.

Nutrient concentration in roots

The root tips (1 cm) that represented new growth in experiments 2, 3, and 4 were collected from the dried samples and digested with HNO_3 for measurement of Al, Ca, Mg, K, and P concentrations using inductively coupled plasma-atomic emission spectroscopy (ICP-AES) analysis.

Statistical analysis

In experiment 1, the effects of various Al concentrations on the root growth were analyzed using one-way analysis of variance (ANOVA), and the significance of difference in treatments were determined by Scheffe's method. In experiments 2 and 4, differences in treatments were analyzed by one-way ANOVA followed by Fisher's least significant difference (Fisher's LSD) test. In experiment 3, differences between −Al and +Al treatments were analyzed by *t*-test.

Table 1. The effects of Al on the shoot and root dry weights and the length of the newly grown roots (experiment 2)

Treatment	Shoot dry weight (g)	Root dry weight (g)	Length of newly grown roots (cm)
Control	4.40 ± 0.46a	5.36 ± 0.41a	1.64 ± 0.12a
−Al	4.49 ± 0.65a	5.49 ± 0.39a	1.75 ± 0.09a
+Al	6.05 ± 0.36b	7.16 ± 0.46b	3.34 ± 0.46b

Data given as mean ± standard error (SE). Values of the shoot and root dry weight are the means of ten seedlings and values of the length of the newly grown roots are the means of 50 roots
Values with lowercase letters indicate a significant difference at $P < 0.05$ according to Fisher's LSD test

Results

Effect of various Al concentrations on growth (experiment 1)

The shoot and root dry biomass and the ratio of root to whole plant biomass (R/T) with various concentrations of Al are shown in Fig. 1. Root biomass increased significantly ($P < 0.05$) with 1.0, 2.5, and 5.0 mM Al treatments as compared with the treatment with control, and of all the treatments, treatment with 2.5 mM Al resulted in the maximum biomass. Shoot biomass also tended to increase with 0.25, 1.0, 2.5, and 5.0 mM Al treatments. The R/T results showed a steady increase with Al concentration from approximately 0.5 mM onward, indicating that the allocation of assimilates to the roots increased with Al treatment and it was significant at 2.5 and 5.0 mM ($P < 0.05$).

Effect of H^+ and Al^{3+} on growth (experiment 2)

The dry weights of the shoots and roots and the average length of the newly grown roots, which appeared after the treatment was initiated, are shown in Table 1. The dry root weight and average length of the newly grown roots significantly ($P < 0.05$) increased with the +Al treatment compared with the control and −Al. Specific morphological changes, such as thickening, white coloration, and good elongation were observed in the roots after treatment with Al.

Effect of intermittent Al treatment on root elongation and rooting (experiment 3)

The root systems were clearly different with the +Al and −Al treatments (Fig. 2). On treatment with −Al, the newly grown roots were observed to be relatively short, less branched, and crowded around the tip of the secondary

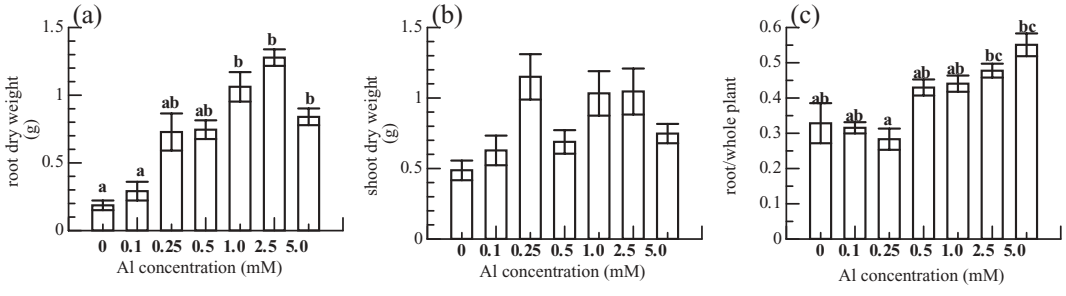

Fig. 1a–c. Effect of various Al concentrations on dry weight of root (**a**) and shoot (**b**) and the dry weight ratio of root to whole plant (**c**) after 9 weeks of treatment (experiment 1). The data are given as the mean ± standard error ($n = 5$). *Different letters* above the bars for each Al concentration indicate a significant difference at $P < 0.05$ according to Scheffe's method

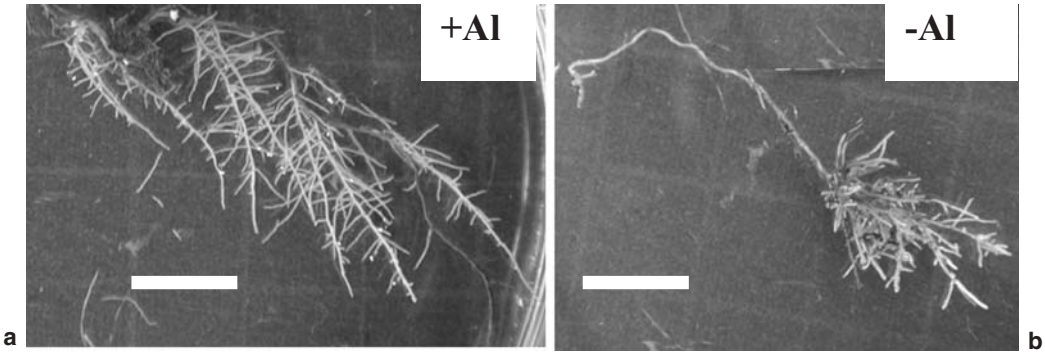

Fig. 2a, b. Intermittent Al treatment effects on rooting and root system. **a** Seedlings were exposed to 2.5 mM Al solution (pH 3.6) for 1 h/day (+Al). **b** Seedlings were exposed to distilled water with pH adjusted to 3.6 with 1 N HCl for 1 h/day (–Al). *Bars* 10 mm

Table 2. The effect of long-term Al treatment on the relative height of shoot and the dry weight of shoot and root (experiment 4)

Treatment	Relative height	Shoot dry weight (g)	Root dry weight (g)
Control	1.21 ± 0.09a	4.84 ± 0.81a	5.29 ± 0.94a
–Al	1.31 ± 0.07a	5.86 ± 0.74a	6.24 ± 0.63a
+Al	2.74 ± 0.15b	23.4 ± 1.59b	15.9 ± 1.67b

Data given as mean ± SE ($n = 5$). The relative heights indicate the ratio of height after 15-month experiment to height before initiation of the experiment
Values with lowercase letters indicate a significant difference at $P < 0.05$ according to Fisher's LSD test

Table 3. Number of roots branching (tertiary roots) from the secondary roots, and the length of the secondary and tertiary roots after 15 months of Al treatment in a sand culture (experiment 4)

Treatment	Number of branched roots	2nd Length of roots	
		Secondary root (cm)	Tertiary root (cm)
Control	13 ± 1.2a	6.02 ± 0.73a	1.37 ± 0.12a
–Al	15 ± 2.5a	8.82 ± 0.89a	2.37 ± 0.20b
+Al	30 ± 2.2b	15.7 ± 1.12b	3.50 ± 0.23c

Values of the root number and lengths of the secondary roots are the mean of 15 roots, and the lengths of the tertiary roots are the mean of 50 roots
Values with lowercase letters indicate a significant difference at $P < 0.05$ according to Fisher's LSD test

root, which had emerged from the taproot. On the other hand, with +Al, the roots were considerably longer and well branched compared with those treated with –Al. The average lengths of the newly grown roots were 0.55 and 5.30 cm with –Al and +Al treatments, respectively, with a significant difference at $P < 0.01$ (data not shown).

Effect of long-term Al effect on growth (experiment 4)

We examined the long-term effects (approximately 15 months) of Al on root growth. The relative height and dry weight of shoot and root were significantly increased by Al treatment ($P < 0.05$; Table 2). Furthermore, they were greater in –Al than in the control, although the increase was not significant. The length of the secondary roots and the number and length of the tertiary roots are shown in Table 3, and the secondary root system is shown in Fig. 3. The greatest increase was observed in the number of tertiary roots after treatment with Al, followed by the –Al and control treatments, and the number of roots with +Al was approximately twice that of the control. The length of the secondary roots also increased with +Al (Table 3).

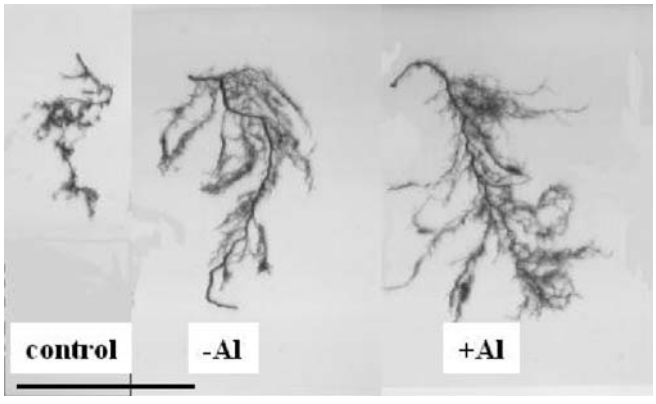

Fig. 3. The effect of a 15-month Al treatment on secondary root systems in sand culture. *Left*, seedlings were given nutrient solution without Al (pH 5.0). *Middle*, seedlings were exposed to nutrient solution with pH adjusted to 3.6 (–Al). *Right*, seedlings were exposed to nutrient solution with Al (pH 3.5) (+Al). *Bar* 10 cm

Nutrient concentration in roots

In all experiments, Al concentration in the root tips was significantly increased after treatment with Al ($P < 0.05$; Table 4). On comparing –Al and +Al treated roots, the concentration of Ca in the root tips was found to be significantly decreased by Al treatment ($P < 0.05$); Mg concentration was significantly decreased by Al in experiment 2 and slightly decreased in experiments 3 and 4. Phosphorus concentration was significantly increased in Al-treated root tips when compared with –Al-treated roots in experiments 3 and 4, and no difference was observed when compared with the results of treatment with –Al in experiment 2.

Table 4. Nutrient concentration in root tips in experiments 2, 3, and 4

Experiment	Treatment	Al (μmol/dw g)	Ca (μmol/dw g)	Mg (μmol/dw g)	K (μmol/dw g)	P (μmol/dw g)
Experiment 2	Control	102 ± 10.6a	188 ± 17.4a	66.4 ± 6.81a	193 ± 28.4b	88.8 ± 7.01a
	−Al	69.0 ± 10.6a	481 ± 49.7b	121 ± 9.48b	528 ± 59.4a	267 ± 28.0b
	+Al	468 ± 53.1b	99.0 ± 9.49a	53.0 ± 8.49a	555 ± 52.6a	231 ± 20.5b
Experiment 3	−Al	39.8 ± 5.99	103 ± 6.92	47.6 ± 1.82	307 ± 13.8	182 ± 17.9
	+Al	334 ± 8.20*	49.2 ± 2.87*	45.1 ± 1.93	278 ± 14.9	412 ± 14.6*
Experiment 4	Control	174 ± 22.6a	281 ± 13.7a	62.8 ± 3.39a	122 ± 11.0a	71.7 ± 8.52a
	−Al	221 ± 25.0a	220 ± 15.1b	47.3 ± 3.65b	112 ± 9.62a	72.2 ± 10.6a
	+Al	583 ± 15.4b	53.2 ± 2.69c	38.8 ± 2.55b	205 ± 10.7b	297 ± 13.0b

Values are given as mean ± SE ($n = 5$)
Values with lower case letters indicate a significant difference at $P < 0.05$ according to Fisher's LSD test in experiments 2 and 4
*Significant difference at $P < 0.05$ based on the t-test

Discussion

It is well known that aluminum is toxic to many plants, although the sensitivity to Al varies among species, the symptoms include the inhibition of root growth and nutrient uptake (Kochian 1995). There are several reports concerning the inhibition of root growth in tree species after treatment with Al. For example, root growth in *Gleditsia triacanthos* L. seedlings was reduced by treatment with 0.6 and 1.5 mM Al for 6 days (Thornton et al. 1986a). The rate of root elongation in *Picea abies* seedlings was inhibited within 24 h after treatment with 0.8 and 1.2 mM Al (Godbold et al. 1988). Thus, Al ions in soil solutions are believed to be a predisposing factor for deterioration of root function and inhibition of nutrient uptake in forest trees (Persson and Majdi 1995). However, based on the results of the four experiments in this study, it was confirmed that in *Quercus serrata*, root growth increases with Al treatment. Osaki et al. (1997) reported that during a hydroponics experiment, Al treatment (approximately 0.6 mM) stimulated root growth and nutrient uptake in plants adapted to low pH soils, such as *Melastoma malabathricum, Melaleuca cajuputi*, etc. In tea plants, which are known to be Al accumulators, root growth was also shown to be stimulated by a nutrient solution containing 0.5 mM Al (Tsuji et al. 1994). In addition, some reports have suggested an increase in root biomass with 0.2 to 2.0 mM Al treatments in non-Al accumulator plants or plants not adapted to strongly acidic soils, such as *Pinus radiata* and *Eucalyptus mannifera* subsp. (Huang and Bachelard 1993), *Acer saccharum* Marsh. (Thornton et al. 1986b), *Quercus rubra* L., and *Fagus grandifolia* Ehrh. (Thornton et al. 1989); and *Pseudotsuga menziesii*, *Larix deciduas*, and *Quercus robur* (Keltjens and Loenen 1989). Kelly et al. (1990) and Keltjens and Loenen (1989) showed that the Al concentration that induced maximum growth differed among tree species. From these reports and the results of this study, it is clear that root growth can be stimulated by Al in several tree species, which include not only Al accumulators but also non-Al accumulators, although the effective concentrations of Al may differ among species.

The mechanism of the effect of Al stimulation on growth has been previously demonstrated. For example, Kinraide et al. (1992) suggested that Al probably ameliorates proton toxicity in roots. In this study, in the case of *Q. serrata*, no difference was observed between the treatment with low pH solutions without Al (pH 3.5) and the control (pH 5.0 or 6.0; Tables 1, 2, and 3). This suggests that the H^+ concentration levels, such as at pH 3.5, are not toxic for *Q. serrata*. On addition of Al at pH 3.5, all the results showed a positive effect of Al on growth. Therefore, it is obvious that Al-induced growth enhancement is not due to the amelioration of H^+ toxicity by Al. The results of experiment 3 indicate that intermittent Al treatment, during which the roots were exposed to the Al solution for 1 h/day for 50 days, stimulated root emergence and root elongation (Fig. 2). This implies that Al adsorption on root surface or apoplast would generate a signal that accelerates growth even if the contact time were short. Although the Ca concentration in root tips was significantly decreased by Al treatment, increase in P concentration in the root tip treated with Al was observed in experiments 3 and 4 (Table 4). A few reports describe the Al-induced decrease in Ca concentration and increase in P in roots of tree species, which show stimulation of root growth by Al (Konishi et al. 1985; Huang and Bechelard 1993). The increase in P concentration has been considered because of the precipitation of P with Al on the root surface or apoplast in root, thereby resulting in P deficiency in plants because of decreased availability (McCormick and Borden 1974). Tsuji et al. (1994) studied the effect of P concentration on root growth with and without Al in nutrient solution using tea and reported that a positive effect of P was not observed without Al. However, remarkable stimulation of root growth was observed in the presence of Al with increased concentration of P. From these results, they suggested that Al plays an important role in the absorption and utilization of P. The increase in P concentration in root tip by Al treatment may result in precipitation with Al, however, tree species that show growth enhancement by Al may have a greater ability to use precipitated P.

During treatments with 0.27 and 2.7 mM Al, specific morphological changes, such as thickening, white coloration, and good elongation of roots, were reported in *Quercus acutissima*, *Cinnamomum camphora*, and *Eucalyptus viminalis* (Oda and Yamamoto 2002). Similar results were also observed in this study. Čížková (1995)

reported that 4 months of treatment with 0.74 and 1.85 mM Al increased the levels of indole-acetic acid (IAA) and cytokinin- and gibberellin-like substances in the roots of *Picea abies*, whereas changes in the levels of these plant hormones correlated with the morphological changes induced by Al, such as inhibition of elongation in the primary roots and stimulation of lateral roots near the primary root apex. In addition to the morphological changes, Oda (2003) reported that the formation of new roots was accelerated by Al treatments in *Q. acutissima* and *C. camphora*, and these phenomena correlated with the constant low concentrations of IAA and increasing concentrations of cytokinin-like substances in roots treated with 2.7 mM Al. From these reports, it is believed that Al-induced root growth enhancement in *Q. serrata* may be correlated with phytohormonal levels in the roots. Al in the rhizosphere might directly or indirectly induce the synthesis or transport of plant hormones such as IAA, cytokinin, and gibberellin.

In this study, it is confirmed that Al enhances *Q. serrata* growth, especially root growth in both the short and long term. We suggest Al may act as a trigger to induce root elongation and rooting. However, whether this phenomenon is due to Al being beneficial for tree growth or due to Al having a role in triggering signal transductions under acidic rhizosphere conditions remains unknown. To understand the mechanisms associated with the positive effect of Al on root growth among tree species, more precise experiments on phytohormones, nutrient balance, and signal transmission are necessary.

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