Root system responses of Japanese red cedar saplings to acidic conditions

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Abstract

Stemflow from Japanese red cedar (Cryptomeria japonica) enters forest soil at a low pH. We evaluated the responses of the root system of Japanese red cedar saplings to acidic conditions, used to simulate this situation, in two different growth media, a brown forest soil (BS) and a Yahagi sand (YS). Soils were acidified by the addition of solutions at pH 2.0, 3.0 and 5.5 (control). Root morphology, root surface area index, root respiration activity and root biomass were measured. In the pH 3.0 treatment, no significant effects were found on the root systems compared with the controls in either soil, except for a slight difference in root-tip diameter in the Yahagi sand. In the pH 2.0 treatment, the surface area index and dry weight ratios of the whole root in the Yahagi sand were significantly lower than those in the other treatments. No significant effects on the whole root were observed in the brown forest soil. These results suggest that detrimental effects of acidic solutions on the root systems would be less significant in brown forest soil, which contains humus, than in the Yahagi sand, which lacks humus. They also suggest that the threshold pH value causing visible morphological changes on the roots of Japanese red cedar saplings falls in the pH range between 2 and 3. White roots in the pH 2.0 treatment had low respiration activity and showed visible morphological changes in both soils. These responses were presumably related to the effects of excess Al in the soil solution. White roots in the pH 2.0 treatment typically produced exodermis. The results suggest that stemflow with a pH of 3.0 has no effects on the root systems of Japanese red cedar, and that the morphology of white roots was adversely affected not by treatment at pH 2.0 but by excess water-soluble Al in the soil. © 2000 Elsevier Science B.V. All rights reserved.

Keywords: Aluminum; Brown forest soil; Cryptomeria japonica; Low pH; Root morphology; Stemflow; White root

1. Introduction

Direct rainfall, throughfall and stemflow constitute the net precipitation on forest soil (White, 1997). The chemical properties of throughfall and stemflow have typical characteristics specific to each tree species (Sassa et al., 1991). It has been...
well established that stemflow on Japanese red cedar (Cryptomeria japonica) has a very low pH (Sassa et al., 1991; Matsura, 1992; Inagaki et al., 1995; Sato and Takahashi, 1996) compared with other Japanese tree species such as Japanese red pine (Pinus densiflora), Japanese larch (Larix leptolepis) and Siebold’s beech (Fagus crenata) (Sassa et al., 1991). For example, the pH values of stemflow on Japanese red cedar ranged from 3.0 to 4.8 in Kumamoto prefecture (western Japan, 32°49′ N, 130°44′ E; Inagaki et al., 1995) and from 2.87 to 3.46 in Kanagawa prefecture (central Japan, 35°26′ N, 139°26′ E; Sato and Takahashi, 1996). The acidified stemflow penetrates the forest soil and lowers the soil pH. Kato and Shirai (1995) reported soil pH (H2O) values around Japanese red cedar stems planted in andosol in the range 3.6–4.8.

Low soil pH can cause leaching of base nutrient cations and increase concentrations of dissolved Al, which is phytotoxic to roots (Foy et al., 1978; Cronan and Grigal, 1995; Marschner, 1995; Clune and Copeland, 1999; Horst et al., 1999). The concentrations of dissolved Al rapidly increase in brown forest soil, red–yellow soil and andosol when the soil pH falls to 4.0 (Miwa et al., 1998). In acidic mineral soil below pH 4.0, Al toxicity may become a greater factor than H+ toxicity (Fitter and Hay, 1981; Marschner, 1991). Little information is available on the effects of acidic conditions (pH ≤ 4.0) on the root morphology. Aluminum toxicity can reduce the root growth of plants and their uptake of essential elements from the soil before symptoms become apparent (Foy et al., 1978; Marschner, 1995). In particular, Al may inhibit calcium uptake by blocking Ca2+ channels in the plasma membrane and inhibit magnesium uptake by blocking binding sites of transport proteins (Horst, 1995; Marschner, 1995). Calcium has essential functions as a bridging element in the apoplasm of root cortical cells leading to morphological changes of the roots (Marschner, 1991). With H+ toxicity, uptake of cations is inhibited by the impairment of the net extrusion of H+ and the decrease of cation loading in the apoplasm (Marschner, 1995).

The objective of this study was to detect the responses of the root system of Japanese red cedar saplings to acidic conditions that simulate the penetration of stemflow with low pH into forest soil. We examined three hypotheses, (1) roots of Japanese red cedar can grow in acidic conditions established by the application of a solution of pH 3.0. Such acidic conditions can be frequently observed around the stems of Japanese red cedar in the field; (2) roots cannot grow and survive in acidic conditions established by the application of a solution of pH 2.0, because of high Al and H+ toxicity. Differences in the responses of roots to acidic conditions between the pH 2.0 and 3.0 treatments can be used to detect the threshold pH causing root injuries; and (3) detrimental effects will be less significant in forest soil, which contains humus, than in gravel or sand lacking humus.

2. Materials and methods

2.1. Plant materials and growth media

We used a 3-year-old Japanese red cedar (C. japonica D. Don) saplings (mean height ca 0.5 m) reared in the nursery of the Aichi Prefecture Forest Experimental Station (Nukata, Aichi prefecture, central Japan: 34°56′ N, 137°21′ E). Japanese red cedar is known to form vesicular–arbuscular mycorrhizas (Karizumi, 1979; Mizoguchi, 1996). Our saplings might have had the mycorrhizas, but we did not evaluate them. The saplings were transplanted individually into plastic pots (Wagner pot, 157-mm diameter; 190-mm high) on 30 June, 1995.

The pots were filled with moderately moist brown forest soil (Forest soil division, 1976) or a Yahagi sand. The brown forest soil was taken from the Aichi Regional Forest of the University of Tokyo. The parent material was granite. The soil had frequently been used as an experimental medium for the evaluation of the effects of soil acidification on Japanese red cedar (Miwa et al., 1994, 1998; Izuta et al., 1997; Hirano and Hijii, 1998). It has a high acid-neutralizing capacity but releases a large amount of Al ions when the pH decreases below 4.0 (Miwa et al., 1998). Yagi et al. (1991) reported the properties of this soil as follows, pH (H2O), 4.3–4.9; exchangeable cations (meq/100 g dw), Ca, 0.11–0.32; Mg,

0.03–0.13; K, 0.08–0.2; Na, 0.05–0.08; cation exchange capacity, 6.9–17.2 meq/100 g dw; total C, 1.5–5.6%; total N; 0.08–0.39%.

Yahagi sand is a riverine gravel from the Yahagi river in Aichi prefecture. It consists of gravel of 2–4 mm diameter and is used as a horticultural medium in Japan. Yahagi sand retained on a 2-mm sieve was washed with dilute hydrochloric acid and deionized water to eliminate soluble cations (nutrients) and humus. We evaluated the effects of acidic solutions on Japanese red cedar roots grown in Yahagi sand in our previous studies (Hirano et al., 1997a,b).

All experiments were performed in a greenhouse on the Nagoya University Campus (Nagoya, Aichi prefecture) to prevent exposure to rain. Shade cloth reduced light intensity to 60% of ambient levels to promote root growth. Average air temperature during the experimental period in the greenhouse was 21.3 ± 0.7°C (mean ± S.E.). Treatments were applied for 15 weeks from 24 August to 6 December, 1995.

2.2. Experimental treatments

The roots of saplings grown in the brown forest soil (BS) and the Yahagi sand (YS) were treated with acidic solutions at three pH levels. Mixed solutions of H2SO4 and HNO3 in a molar ratio of 2:1 were used to create the pH 2.0 treatment (abbreviated BS2 and YS2) and the pH 3.0 treatment (BS3, YS3). The pH was adjusted by adding deionized water to each solution. Deionized water at pH 5.5 was used as the control treatment (BSC, YSC). Twice a week, in the evening, 300 ml of solution was applied to the soil in each pot. Care was taken not to expose the above-ground plant parts to the solutions. Because of the lower water-holding capacity of the Yahagi sand, about two-thirds of the applied solution leached out of the pots. Throughout the treatment period, pots were supplied with liquid fertilizer every 3 weeks for brown forest soil (NH4–N, 1.95; NO3–N, 0.90; (NH4)2CO–N, 2.15; P, 10; K, 5.0 mg/pot week) and every week for Yahagi sand (NH4–N, 5.85; NO3–N, 2.70; (NH4)2CO–N, 6.45; P, 30; K, 15 mg/pot week).

Eight saplings were subjected to each treatment. The total volume of solution added to each pot during the treatment period corresponded to an annual (52 weeks) precipitation of about 1560-mm (roughly equivalent to the average annual precipitation that would be encountered by these saplings in the forest in Japan).

2.3. Plant biomass and root analysis

After the experimental period, saplings were carefully harvested to avoid injuring their root systems. They were separated into foliage, stem, white roots (newly grown roots) and other roots. White roots are defined as unsuberized roots that are clearly white (Karizumi, 1979). They were distinguished visually from other roots (Hirano and Yokota, 1996). The whole root was defined as white roots plus other roots and used to evaluate the entire roots of one sapling. Roots were thoroughly rinsed with running deionized water until they were free of soil mix. The samples were oven-dried at 80°C for 48 h to determine their dry weight. The dry weight ratio for each sapling was defined as the ratio of the dry weight of each organ to the total dry weight of the sapling.

The root surface area index was estimated by using a modified gravimetric method, which provides an accurate measurement of the relative surface areas of roots and has the advantage of being rapid and inexpensive (Carley and Watson, 1966). The method uses calcium nitrate, which is moderately heavy, highly soluble in water and neither corrosive nor toxic. We modified the method to directly measure the weight of Ca(NO3)2 attached to the root surface, instead of measuring the loss of weight of the solution. Five root systems per treatment were air-dried and weighed separately on a microbalance (W1). Each root system was dipped into 2 M Ca(NO3)2 for 15 s and then lifted above the solution. After being drained for 30 s, each root system was weighed again (W2). The root surface area index was calculated as follows:

Root surface area index (g Ca(NO3)2/g dw) = \( \frac{W_2 - W_1}{\text{Root dry weight}} \)
Before oven-drying, white roots were carefully studied under a stereomicroscope to verify their color and determine the presence of visible changes. Fifteen root tips (50-mm long) from each of three saplings (45 root tips per treatment) were randomly selected for morphological analysis of the white roots. The maximum diameters of these root tips were measured directly. The respiration activity of the white roots from three saplings was measured by the \( \alpha \)-naphthylamine method (Yoshida, 1966). This approach assumes that the extent of \( \alpha \)-naphthylamine oxidation serves as an index of the level of peroxidase activity, which in turn correlates positively with root respiration rates. About 1 g fw of white roots from each root system was sampled and placed in a Erlenmeyer flask, and 50 ml of 20 mg l\(^{-1}\) \( \alpha \)-naphthylamine solution was added. The flask was shaken slightly and allowed to stand for about 10 min. Then the first sample (2 ml) was taken from it to measure the first concentration of \( \alpha \)-naphthylamine. The remainder of the solution was shaken at 25°C for 4 h, and the last sample was taken to measure the last concentration of \( \alpha \)-naphthylamine. Next 10 ml of distilled water, 1 ml of 1% (w/v) sulfanilic acid solution and 1 ml of 100 mg l\(^{-1}\) sodium nitrite solution were added to the sample for coloration, and more distilled water was added until the total volume reached 20 ml. The absorbency at 510 nm was measured with a spectrophotometer. The respiration activity of the white roots was represented as the extent of \( \alpha \)-naphthylamine oxidation per unit dry weight of white roots per h (\( \mu \)g/g dw h).

2.5. Properties of the soils

After the experimental period, two 20-g oven-dry soil samples from each of three pots per treatment were taken to determine the soil pH (H\(_2\)O) and the concentrations of water-soluble cations in the soil. The pH (H\(_2\)O) of the solutions (dry soil, H\(_2\)O = 1:2:5 [w/w]) was measured with a pH meter. The concentrations of Ca and Mg in the solution (dry soil, H\(_2\)O = 1:5 [w/w]) were determined by atomic absorption spectrophotometry, and the concentrations of K and Na were determined by flame photometry.

2.6. Statistical analysis

The percentage nutrient concentrations in the new foliage and in the white roots and the dry weight ratios were arcsine-transformed. The transformed data were analyzed by one-way analysis of variance (ANOVA), and the means were compared with Tukey’s honestly significant difference (HSD) test (Norussis, 1997).

3. Results

3.1. Effects on the overall sapling root systems

No visible injuries on the foliage or stem were observed in any treatment. In the brown forest soil, no significant differences were found in the dry weight ratios of foliage, stem, or the whole root between the control (BS2) and the two acidic treatments (BS2, BS3; \( P < 0.05 \); Table 1). However, the dry weight ratio of the white roots in the pH 2.0 treatment (BS2) was significantly lower than in the control (\( P < 0.05 \); Table 1).

In the Yahagi sand, there was a significant difference in the dry weight ratio of foliage between the pH 2.0 treatment (YS2) and the control. The dry weight ratios of the whole root and white roots in the pH 2.0 treatment (YS2) were significantly lower than those in the pH 3.0 treatment (YS3) and the control (\( P < 0.05 \); Table 1).

In both soils, the results of the surface area indexes of the whole root showed the same effects as shown for the dry weight ratio of the whole
root (Table 1). There were no significant differences in this index in the brown forest soil between the acidic (BS2, BS3) and control (BSC) treatments \((P > 0.05)\). In the Yahagi sand, however, the index for the pH 2.0 treatment (YS2) was significantly lower than those for the pH 3.0 treatment (YS3) and the control \((P < 0.05)\).

3.2. Morphological changes in white roots

The white roots in the pH 2.0 treatment in both soils (BS2, YS2) exhibited distinct morphological changes. One of the most interesting changes was that the roots had many stunted tips and produced some exodermis (Fig. 1). The maximum root-tip diameters in both pH 2.0 treatments (BS2, YS2) were significantly larger than those in the pH 3.0 (BS3, YS3) and control treatments \((P < 0.05; \text{Fig. 2})\). The respiration activity of these white roots was significantly lower than in the pH 3.0 (BS3, YS3) and control (BSC, YSC) treatments \((P < 0.05; \text{Fig. 3})\).

The white roots in both soils in the pH 3.0 treatment (BS3, YS3) were well developed, and appeared similar to those in the controls. There were no significant differences between the pH 3.0 treatments (BS3, YS3) and the controls (BSC, YSC) in the dry weight ratio or respiration activity of the white roots \((P > 0.05; \text{Table 1, Fig. 3})\).

3.3. Nutrient status

Table 2 shows the concentrations of P and Al in the new foliage and white roots of the saplings. Although there were no significant differences in the P concentrations of white roots between the acidic treatments (BS2, BS3, YS2, YS3) and the corresponding controls (BSC, YSC), the concentration of P was significantly lower in new foliage of saplings grown in both soils in the pH 2.0 treatment (BS2, YS2) than in the controls (BSC, YSC; \(P < 0.05\)). The Al concentrations of the roots in the pH 2.0 treatments (BS2, YS2) tended to be higher than those in the pH 3.0 (BS3, YS3) and control (BSC, YSC) treatments, though this was significant only in the brown forest soil.

3.4. Properties of the soils

The concentrations of water-soluble cations (Ca, Mg, K) in the brown forest soil were significantly higher in the pH 2.0 treatment (BS2) than in the other treatments (BS3, BSC; \(P < 0.01\); Table 3). No such differences were observed in the

| Table 1 | Dry weight ratios of the foliage, stem, the whole root (white roots plus other roots), white roots and other roots, and root surface area index of the whole root, of Japanese red cedar saplings treated with acidic solutions (mean ± S.D.)^a |
|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|
|                | Foliage         | Stem            | Whole root      | White roots     | Other roots     | Root surface area index (g Ca(NO₃)₂/g dw) |
| **Brown forest soil** |                 |                 |                 |                 |                 |                                           |
| BS2             | 56.1 ± 4.5a     | 13.2 ± 2.5a     | 30.7 ± 4.0a     | 6.8 ± 1.2a      | 23.8 ± 4.0a     | 1.22 ± 0.20a |
| BS3             | 54.6 ± 4.5a     | 13.2 ± 2.3a     | 32.2 ± 3.4a     | 8.8 ± 1.5ab     | 23.4 ± 4.1a     | 1.31 ± 0.10a |
| BSC             | 52.9 ± 4.9a     | 12.0 ± 2.5a     | 35.1 ± 6.4a     | 10.7 ± 2.7ab    | 24.5 ± 4.7a     | 1.30 ± 0.20a |
| **Yahagi sand** |                 |                 |                 |                 |                 |                                           |
| YS2             | 57.0 ± 3.4a     | 14.5 ± 1.4a     | 28.5 ± 3.5a     | 5.9 ± 1.0a      | 22.6 ± 3.9a     | 1.14 ± 0.24a |
| YS3             | 53.6 ± 2.1ab    | 13.7 ± 2.1a     | 32.8 ± 2.7ab    | 10.5 ± 2.3ab    | 22.2 ± 2.9a     | 1.42 ± 0.15ab |
| YSC             | 50.9 ± 2.7b     | 14.2 ± 1.2a     | 34.9 ± 3.4b     | 11.0 ± 2.1b     | 23.9 ± 2.6a     | 1.45 ± 0.13b |

^a Each value represents the mean of eight (dry weigh ratio) or five (root surface area index) measurements. Values within the same column for each soil followed by the same letter are not significantly different according to Tukey’s HSD test \((P > 0.05)\). BS2 = pH 2.0 treatment in the brown forest soil; BS3 = pH 3.0 treatment in the brown forest soil; BSC = control (pH 5.5) treatment in the brown forest soil; YS2 = pH 2.0 treatment in the Yahagi sand; YS3 = pH 3.0 treatment in the Yahagi sand; YSC = control (pH 5.5) treatment in the Yahagi sand.
Yahagi sand. The decrease in the pH in the Yahagi sand (from 5.4 in the control to 3.9 in the pH 2.0 treatment) was greater than that in the brown forest soil (from 4.3 in the control to 3.4 in the pH 2.0 treatment; Table 3).

4. Discussion

In the brown forest soil, the dry weight ratio, respiration activity and morphology of the white roots were all significantly affected by the application of acidic solutions of pH 2.0, but no significant effects were found for the surface area index or dry weight ratio of the whole root (Table 1, Figs. 1–3). In the Yahagi sand, both the white roots and the whole root were significantly affected by the pH 2.0 treatment. These results support our third hypothesis: the detrimental effects on the root system of the application of acidic solution would be less significant in the brown forest soil, which contains humus, than in Yahagi sand, which lacks humus. These results also imply that the detrimental effects on white roots were spread throughout the whole root system. This indicates that the white roots were the first organs to be affected by acidification stress.

In the pH 3.0 treatment, no significant effects were found on the root systems in the brown forest soil (Table 1, Figs. 2 and 3). In the Yahagi sand, the difference in root-tip diameter was only about 0.1 mm between the pH 3.0 treatment and the control (Fig. 2). The results
support the first hypothesis that white roots can grow in the acidic conditions in the pH 3.0 treatment. Sato and Takahashi (1996) reported that the annual average pH of stemflow was 3.11 in Kanagawa prefecture. Our results suggest that acidic solutions at pH values around 3 would not detrimentally affect the root systems.

In the pH 2.0 treatment in both soils (BS2, YS2) to detect the threshold pH value causing root injuries, the dry weight ratios of white roots were significantly lower than in the controls, but the white roots survived and developed (Table 1). Therefore, our second hypothesis was rejected. The results suggest that the threshold pH value causing visible injuries on the roots of Japanese red cedar saplings treated with acidic solutions falls in the pH range between 2 and 3.

The most noticeable responses of the white roots to the pH 2.0 treatment were that the root tips had some exodermis, branching ceased and root tips were darkened (Fig. 1). The presence or absence of an exodermis and the timing of such morphological changes when plants are moved from pH 2.0 treatment to the control (amelioration of acidic conditions) and vice versa (deterioration of conditions) may be important in evaluating the responses of roots to environmental changes. The colonization of roots by vesicular–arbuscular mycorrhizal fungi can result in significant alteration of tree root morphology (Hooker and Atkinson, 1996). However, we did not evaluate the status of the mycorrhizas. Further studies are required to determine how exodermis is produced over roots and whether it is related to the presence or absence of mycorrhizal fungi.

Another response of the white roots in the pH 2.0 treatment was that they were thickened in both soils (Fig. 2). In various conifers subjected to stress caused by excess Al, stunted, darkened and thick-
ened root tips are well-known phenomena (Schier, 1985; Schier and McQuattie, 1998; Schier et al., 1990; Cronan et al., 1989; Schaedle et al., 1989; McQuattie and Schier, 1990, 1992). Similarly, increasing the concentration of Al caused an increase in the diameter of the white root tips of Japanese red cedar saplings grown in glass beads (Hirano and Hijii, 1998). Moreover, in this study, we found an increased Al concentration in the white roots and a decreased P concentration in the new foliage in the pH 2.0 treatment in both soils (Table 2). In Japanese red cedar, it has commonly been observed that excess Al reduces the P concentration in shoots and increases the Al concentration in the roots (Miyake et al., 1991; Kohno et al., 1995; Izuta et al., 1996). The detrimental effects on the white roots in our study occurred at a soil pH 3.4 in the brown forest soil (BS2), whereas no significant effects were observed with the soil at pH 3.9 (BS3; Table 3). Miwa et al. (1994) reported that the concentration of water-soluble Al in brown forest soil was > 500 µg/g dry soil at a soil pH 3.4 compared with about 50 µg/g dry soil at pH 3.9. These results

Table 2
Concentrations of P and Al in the new foliage and white roots of Japanese red cedar saplings treated with acidic solutions (mean ± S.D.)

<table>
<thead>
<tr>
<th></th>
<th>Concentration in new foliage (%)</th>
<th>Concentration in white roots (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>P</td>
<td>Al</td>
</tr>
<tr>
<td><strong>Brown forest soil</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>BS2</td>
<td>0.11 ± 0.01&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.01 ± 0.00&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td>BS3</td>
<td>0.12 ± 0.01&lt;sup&gt;ab&lt;/sup&gt;</td>
<td>0.01 ± 0.01&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td>BSC</td>
<td>0.13 ± 0.01&lt;sup&gt;b&lt;/sup&gt;</td>
<td>0.01 ± 0.00&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td><strong>Yahagi sand</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>YS2</td>
<td>0.26 ± 0.06&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.01 ± 0.00&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td>YS3</td>
<td>0.40 ± 0.09&lt;sup&gt;b&lt;/sup&gt;</td>
<td>0.01 ± 0.00&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td>YSC</td>
<td>0.44 ± 0.06&lt;sup&gt;b&lt;/sup&gt;</td>
<td>0.01 ± 0.00&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
</tbody>
</table>

<sup>a</sup> Each value represents the mean of four measurements. Values within the same column for each soil followed by the same letter are not significantly different according to Tukey’s HSD test (P > 0.05). Treatment abbreviations are the same as in Table 1.

Table 3
Water-soluble cation concentrations and soil pH in the brown forest soil (BS) and the Yahagi sand (YS) treated with acidic solutions (mean ± S.D.)

<table>
<thead>
<tr>
<th></th>
<th>Concentration (meq per 100 g dry soil)</th>
<th>pH (H&lt;sub&gt;2&lt;/sub&gt;O)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Ca</td>
<td>Mg</td>
</tr>
<tr>
<td><strong>Brown forest soil</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>BS2</td>
<td>0.224 ± 0.034&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.072 ± 0.011&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td>BS3</td>
<td>0.033 ± 0.000&lt;sup&gt;b&lt;/sup&gt;</td>
<td>0.018 ± 0.004&lt;sup&gt;b&lt;/sup&gt;</td>
</tr>
<tr>
<td>BSC</td>
<td>0.015 ± 0.006&lt;sup&gt;b&lt;/sup&gt;</td>
<td>0.006 ± 0.004&lt;sup&gt;b&lt;/sup&gt;</td>
</tr>
<tr>
<td><strong>Yahagi sand</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>YS2</td>
<td>0.002 ± 0.002</td>
<td>N.D.</td>
</tr>
<tr>
<td>YS3</td>
<td>N.D.</td>
<td>N.D.</td>
</tr>
<tr>
<td>YSC</td>
<td>N.D.</td>
<td>N.D.</td>
</tr>
</tbody>
</table>

<sup>a</sup> Each value represents the mean of three measurements. Values within the same column for each soil followed by the same letter are not significantly different according to Tukey’s HSD test (P > 0.05). Treatment abbreviations are the same as in Table 1. N.D., not detected.
suggested that the morphological changes that we observed in the white roots in both soils resulted from the effects of an excess of water-soluble Al in the soil.

The results of this study suggest that stemflow at a low pH of around 3.0 from Japanese red cedar in the field has no effect on the root system, and that morphological changes are induced not by the acidity of the solution but by an excess of water-soluble Al in the soil. The effects of Al on the roots are particularly dramatic; even at a concentration of only about 0.37 mM, Al significantly reduced the root biomass of Japanese red cedar seedlings (Izuta et al., 1996). Further studies are required to determine the threshold Al concentration or the Ca/Al molar ratio at which Al begins to affect white roots (Cronan and Grigal, 1995; Sato, 1997; Hirano et al., 2000) and to stimulate the formation of exodermis on them. Also interesting would be observing whether morphological changes of white roots in response to Al in the forest soil occurred on Japanese red cedar trees grown in the field.

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