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ORIGINAL ARTICLE

Radial movement of sapwood-injected rubidium into heartwood of Japanese cedar (*Cryptomeria japonica*) in the growing period

Naoki Okada · Yasuhiko Hirakawa · Yukio Katayama

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Abstract Rubidium solution was injected in the sapwood of a Japanese cedar cultivar in the growing period, and its radial movement in stem was traced to investigate the accumulation of alkali metals in the heartwood. Sapwood-injected Rb was detected in outer heartwood at 10 days after the treatment, and continued increasing at 20 days after. Radial movement of Rb toward heartwood was considered to occur soon after the treatment, and to decline at a certain point of the time after Rb injection ceased. However, Rb continued moving in heartwood probably by diffusion even after the cease of Rb injection. In a series of injection experiment, radial movement of injected Rb is not corresponding to the seasonality of both cambial activity and cytological changes of ray parenchyma accompanied with heartwood formation. From the results on Rb's behavior, we conclude that accumulation of K and other alkali metals in heartwood of Japanese cedar has two steps, active transport from sapwood to outer heartwood via ray, and diffusion in heartwood, and that these processes proceed independently from both cambial activity and cytological changes of ray parenchyma.

Keywords Rb · Alkali metals · Active transport · Diffusion · Black heartwood

Introduction

Radioisotopes have been a useful tool in the stem injection technique [1–3]. It is applicable to investigate the movement of water, nutrients and metabolites in trees by labeling the target atoms or molecules. Unfortunately, the use of radioactive tracers in the field is nowadays restricted or not allowed. Instead, non-radioactive tracers, such as stable isotopes and activable tracers, are being the alternative. In the previous study [4], we applied activable tracers (Rb and Eu) to investigate mineral movement in Japanese cedar (*Cryptomeria japonica*) stems, especially movement between sapwood and heartwood. Present study is a further approach using rubidium (Rb) as an activable tracer. Rb has similar chemical properties as K, whose accumulation in heartwood of Japanese cedar is considered to have close relation with black heartwood [5–8]. Investigating the movement of Rb in the stem of Japanese cedar will give a clue to the phenomenon.

In our previous study [4], we traced the movement of sapwood-injected Rb and Eu in Japanese cedar in the resting period for up to 204 days. The results indicated that Rb injected in the sapwood was detected in the heartwood at 40 days after the treatment, whereas Eu was not. The radial movement of Rb from the sapwood to the heartwood was considered to be not by diffusion but by active transport through the ray; this process was more clearly observed in the Japanese cedar cultivars having large amount of moisture in heartwood than in those having small amount of moisture in heartwood. However, we have not yet confirmed the seasonality of Rb movement and the

N. Okada · Y. Hirakawa
Forestry and Forest Products Research Institute, P.O. Box 16, Tsukuba Norin Kenkyu Danchi-nai, Ibaraki 305-8687, Japan

N. Okada (✉) · Y. Katayama
Graduate School of Agriculture, Kyoto University, Kyoto 606-8502, Japan
e-mail: okad@kais.kyoto-u.ac.jp

Y. Katayama
Division of Human Environment, University of Human Environments, Okazaki, Aichi 444-3505, Japan

rate of radial movement. In this study, we applied the same technique in the growing period to a Japanese cedar cultivar having large amount of moisture in heartwood. The purpose is to investigate how rapidly the element moves from the sapwood to the heartwood in the growing period, and is to discuss the role of alkali metals, especially K, accumulated in heartwood of Japanese cedar based on the behavior of injected Rb.

Materials and methods

Materials

Since heartwood property, such as ash and moisture content, of Japanese cedar is reported to be affected by genetic factors [5], selection of cultivar for the experiment is of particular importance. Kumotooshi, a cultivar known to have large amount of moisture in heartwood [6], was used in this study, because the cultivars forming such heartwood tend to accumulate K in their heartwood [5, 7, 8], and are expected to also accumulate Rb, one of alkali metals as K. Six trees (KT1–KT6) growing in the National Tree Breeding Center (now the Forest Tree Breeding Center, Forestry and Forest Products Research Institute), Mito, Ibaraki Prefecture. They were same age (ca. 30 years old) and similar height (ca. 21 m).

Rb injection and sample collection

Each sample tree was injected with 500 ml of RbCl solution (100 mM) at around 1.7 m above the ground on May 19, 1995. A plastic bottle filled with the solution was set at about 20 cm higher position than the injection point of the stem. The solution was introduced into a drilled hole (3 mm ϕ) through a Tygon tube (inner diameter = 2 mm) with a stainless tube at its end. The drilled depth was 2 cm, because sapwood width of the Japanese cedar individuals of similar size in the site was around 4 cm. We confirmed after felling the tree that the stainless tube reached nearly the middle of sapwood region. Almost all the solution was injected into KT1, KT2 and KT4 within 3 days, and into KT3 and KT6 within 20 days. About 160 ml of the solution was remained in the plastic bottle attached to KT5 at 20 days since the start of injection. Two trees (KT1 and KT2) were felled at 10 days after the treatment and two trees (KT3 and KT4) at 20 days after. The last two trees (KT5 and KT6) were felled on November 7, 1995, 172 days after the treatment. At this time, there was no solution in the bottle attached to KT5.

Four disks, each of which was 20 cm thick, were collected from each tree at +0, +2, +4 and +6 m above the injection height in the field. After removing both cross surfaces of each disk in laboratory, one wood block was cut out from the injection side of each disk for the determination of Rb content. Three sections from the sapwood and four sections from the heartwood were cut out from each wood block (Fig. 1). The sizes of the sections were 10 mm (*L*) × 10–15 mm (*R*) × 2 mm (*T*). Inner most section of sapwood (S3 in Fig. 1) included white zone. Wood sections collected at +0 m position were located at 5 cm above the injection point. Because of the limitation of available trees, we estimated the background content of Rb using injected trees as follows. Wood blocks were cut from the disks of KT5 and KT6 at the height of +0 m to determine the background of Rb content in the wood. They were obtained from the opposite side of the injection point in each disk. Seven wood sections, three of which were from the sapwood, were cut out from each wood block (Fig. 1).

Moisture content of heartwood was determined using disks separately collected at a similar height to that of sample disks for tracer analysis. Pith-to-cambium strip [20 mm (*L*) × 30 mm (*T*)] was cut out from each disk, and then heartwood was separated. After oven-drying at 105°C for more than 24 h, moisture content of each heartwood sample was calculated.

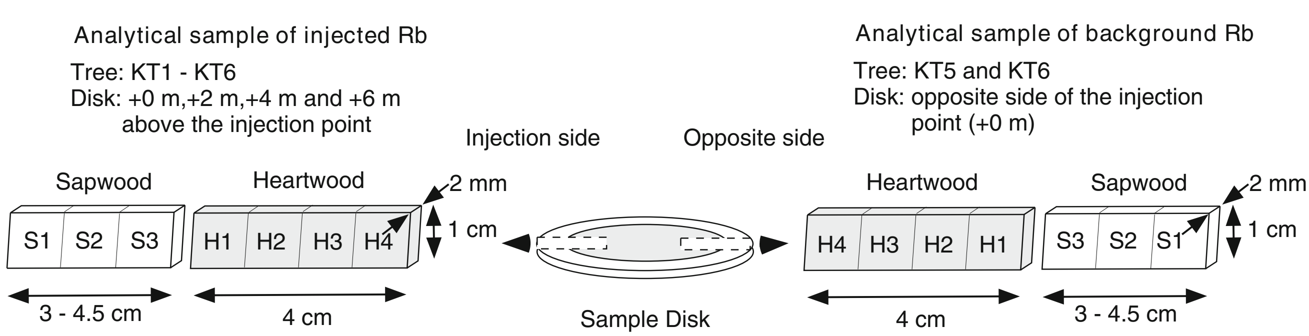


Fig. 1 Schematic diagram of sample preparation for determination of Rb. Sections of *S1–S3* are from sapwood, and *H1–H4* are from heartwood. Section *S3* includes white zone

Table 1 Moisture content in the heartwood of Kumotooshi cultivar (KT)

KT1		KT2		KT3		KT4		KT5		KT6	
HAB (m)	MC (%)	HAB (m)	MC (%)	HAB (m)	MC (%)	HAB (m)	MC (%)	HAB (m)	MC (%)	HAB (m)	MC (%)
1.2	196.5	1.2	202.8	1.6	165.8	2.3	191.2	1.4	196.9	1.4	223.5
3.8	184.6	3.8	154.6	3.6	171.2	4.3	175.6	3.4	142.9	3.4	168.2
5.8	145.2	5.8	155.1	5.6	132.6	6.3	161.2	5.4	141.1	5.4	136.5
7.8	158.0	7.8	129.0	7.6	126.2	8.3	139.5	7.4	132.3	7.4	118.1

Activable tracers were injected into the stem at around 1.7 m above the ground except KT4. Injected height of KT4 was 2.1 m above the ground

HAB Height above the ground, *MC* moisture content

Determination of activable tracers

Rubidium content in wood sections was determined by instrumental neutron activation analysis as described in an earlier report [9]. Neutron irradiation and γ-ray spectrometry were conducted at the Reactor Research Institute, Kyoto University, the Radioisotope Research Center, Kyoto University, and the Institute of Atomic Energy, Rikkyo University. Potassium content was also determined to use the ratio, Rb/K, as the indication of the Rb movement.

Results

Heartwood moisture and background Rb content in Kumotooshi

Moisture content in the heartwood of Kumotooshi cultivar ranged from 118 to 223% (Table 1). The heartwood moisture contents became smaller with increasing height, but lower heartwood contained much amount of moisture exceeding 150%, except at 5.8 m of KT5. Thus, we judged the sample trees met the requirement of this study. Rubidium contents in the opposite side to the injection point of KT5 and KT6 are shown in Table 2 together with K contents and Rb/K. Rubidium content ranged from 2.1 to 3.5 ppm in the sapwood and from 5.4 to 6.2 ppm in the heartwood of the two trees. The Rb content in the heartwood was as similar as those reported for Japanese cedar [10, 11], and the background in our previous report [4]. Potassium contents in the two trees were much higher than those of Rb, but their distribution patterns, increasing from outer to inner sapwood and almost constant in heartwood region, were very similar to the Rb's. The value of Rb/K was, accordingly, rather constant especially in the heartwood, and the range (0.0022–0.0027) was lower than the background in our previous report [4]. We, therefore, judged that the Rb content in the wood of the opposite side was not influenced by Rb injection. There was no significant difference in mean value of Rb/K in heartwood between KT5 (0.0025 ± 0.0002) and KT6 (0.0024 ± 0.0002) in t test ($t = 1.221$, $P = 0.268$). Thus, we adopted the mean value of two trees (Rb/K = 0.0025) as the background in the heartwood of the Kumotooshi cultivar in the later discussion.

Table 2 Background Rb and K contents, and Rb/K at the breast height in Kumotooshi cultivar

Sample	Rb (ppm)	K (ppm)	Rb/K
KT5			
S1	3.4	650	0.0052
S2	2.8	700	0.0040
S3	3.5	1300	0.0027
H1	5.6	2100	0.0027
H2	5.7	2100	0.0027
H3	6.0	2400	0.0025
H4	5.9	2500	0.0024
KT6			
S1	2.1	740	0.0028
S2	2.2	720	0.0031
S3	3.1	1100	0.0028
H1	5.4	2500	0.0022
H2	6.0	2400	0.0025
H3	6.2	2400	0.0026
H4	6.0	2500	0.0024

S1–S3 Sapwood from outer to inner part, *H1–H4* heartwood from outer to inner part

Rubidium distribution at 10 and 20 days after the treatment

At 10 days after the treatment, Rb content in the outermost sapwood (S1 in Fig. 2) was the greatest in each height except at the +2 m of KT1, and rapidly decreased toward the innermost sapwood. The concentrations were greater than ten times of those of the sapwood background in Table 2. Rubidium content in the heartwood was also the greatest at the outermost part (H1, up to 100 ppm in KT1), and less rapidly decreased inward than in the sapwood. The concentrations were up to ten times greater than those of

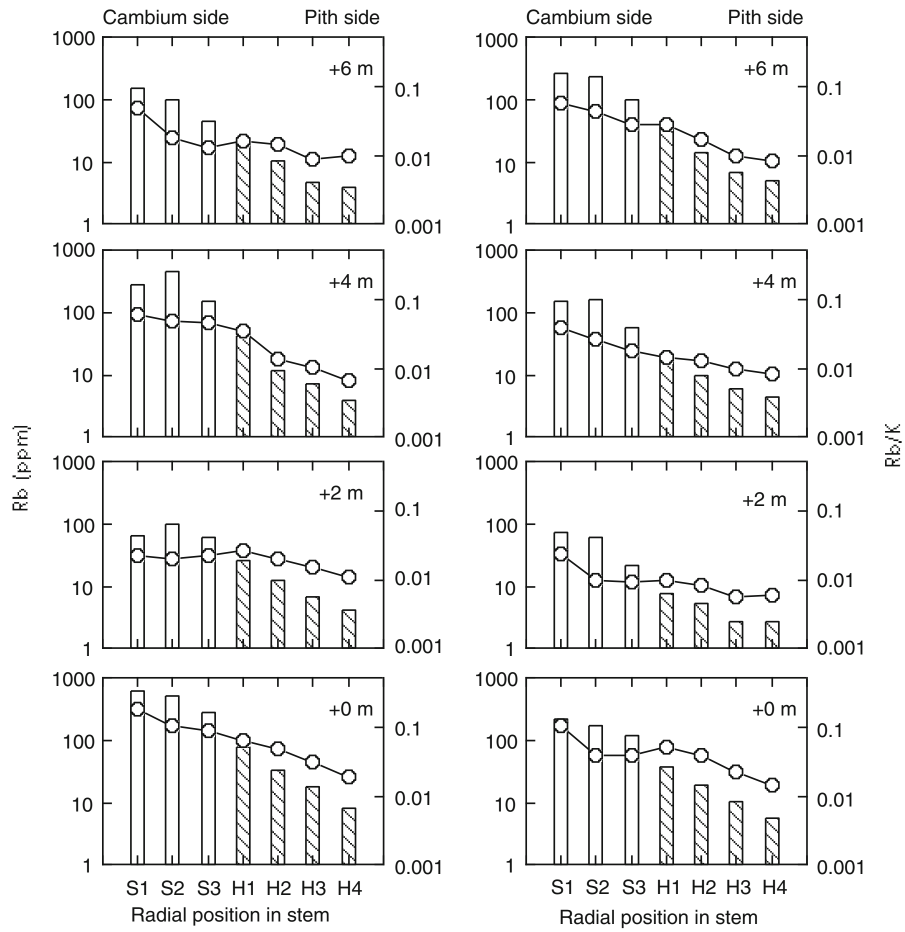


Fig. 2 Rb content and Rb/K in Rb-injected Kumotooshi cultivar at 10 days after the treatment. KT1 (*left*) and KT2 (*right*). Note that *vertical axes* are in logarithm to compare the wide range of Rb content and Rb/K among Figs. 2, 3 and 4. *Circles* Rb content, *white bars* Rb/K in sapwood, *gray bars* Rb/K in heartwood

the heartwood in Table 2, but there was not so much difference between the innermost parts (H3 and H4).

At 20 days after the treatment, the radial distribution of Rb showed slightly different pattern from that at 10 days after, although the two patterns kept a decreasing trend towards inner part (Fig. 3). Rubidium content in the outermost sapwood was not much greater in the sapwood region. Rubidium content in the outermost heartwood (H1) was greater than that in the adjacent sapwood (S3) except one radius (at +0 m in KT4) as a result of further supply of Rb from the sapwood.

The Rb/K values in the heartwood at the two sampling time showed the decreasing trend from the outer part (H1) to the inner (H4) in accord with the similar changes of Rb concentrations. All the values were greater than the background value (Rb/K = 0.0025) except H3 and H4 at +2 m in KT2.

Rubidium distribution at 172 days after the treatment

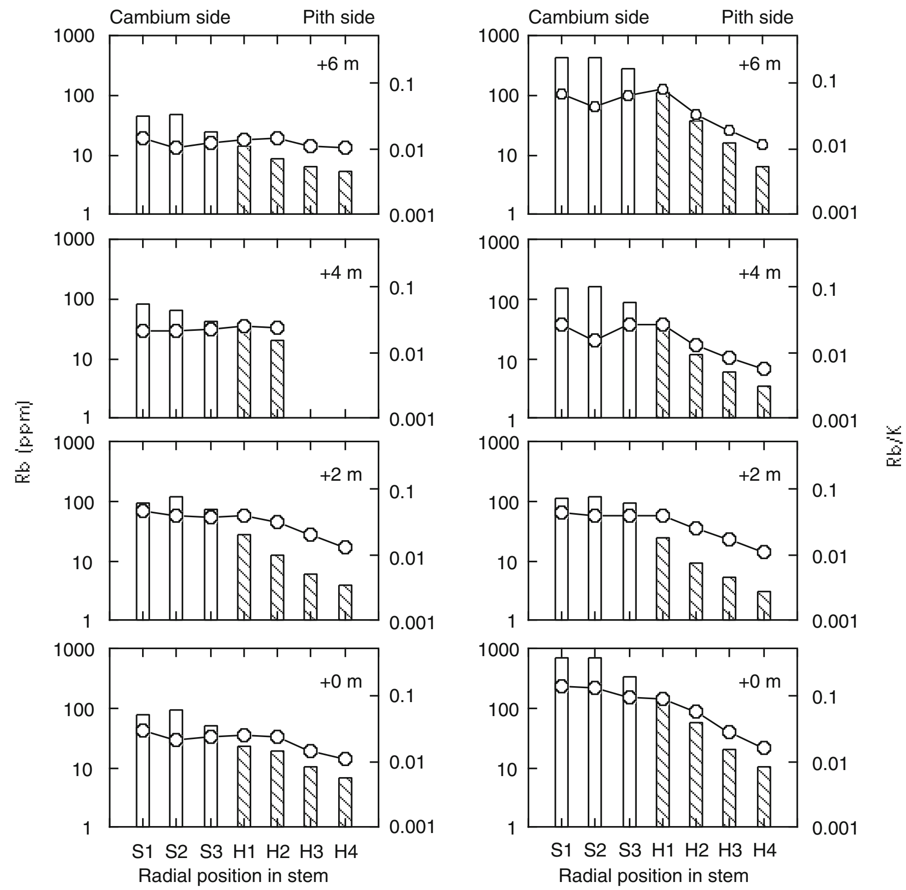
The radial distribution pattern of Rb at 172 days after the treatment (Fig. 4) was quite different from those observed at 10 and 20 days after. A decreasing trend of the Rb content from the outer part to the inner part was no longer observed, and the Rb content in the sapwood region became smaller than that in the heartwood region. In most of the cases, the highest concentration of Rb was observed at the outer heartwood (H1 or H2), but there was less difference of Rb content within heartwood compared with the difference observed at 10 and 20 days after (Figs. 2, 3). The Rb/K value in the heartwood region still showed a decreasing trend from H1 to H4, but the decreasing rate was much smaller than those in Figs. 2, 3 corresponding to the less difference of Rb content in the region.

Discussion

Rate of Rb movement in radial direction in the stem of Japanese cedar

Rubidium injected at the center of sapwood region moved up with transpiration stream (Fig. 2). Fraser and Mawson [1] reported that radioactive ^{86}Rb injected into yellow birch stem in July was detected at 10 feet (ca. 305 cm) high above the injection point within 10 min, and was detected

Fig. 3 Rb content and Rb/K in Rb-injected Kumotooshi cultivar at 20 days after the treatment. KT3 (*left*) and KT4 (*right*). Note that *vertical axes* are in logarithm. *Circles* Rb content, *white bars* Rb/K in sapwood, *gray bars* Rb/K in heartwood



at 15 feet (ca. 457 cm) high within 24 h. Beside the rapid upward movement at the initial stage, they found the upward pathway as a narrow channel of about 1 inch (2.54 cm) in width along the grain. This is consistent with the observations in injection experiments for Japanese cedar in this study and in Aoki et al. [12], in which dark-colored stain up to 2 cm wide in both radial and tangential directions appeared in the center of sapwood region of injected trees. In their Sr injection experiment, Aoki et al. [12] found that little Sr was detected outside the stained area, and concluded that the radial movement of injected Sr is small, and that there is almost no tangential movement. The behavior of injected Rb in sapwood region of Japanese cedar is, therefore, described as upward movement caused by transpiration stream, and horizontal movement in narrow region probably caused by diffusion. Since mineral cations in green wood are adsorbed to wood exchange sites [13–15], or form complexes [14], injected Rb becomes gradually immobile in sapwood. Fraser and Mawson [1] reported that radioactivity of injected ^{86}Rb became fairly uniform throughout its path of movement at the end of 3 days since injection. The observation seemed to indicate that injected Rb reached an adsorption/desorption equilibrium on exchange sites along the path.

Figure 2 indicates that Rb injected in sapwood already exists in the outer heartwood at 10 days after the treatment. It is difficult to estimate exactly when the injected Rb started to relocate to the heartwood, but increases in Rb content and Rb/K in heartwood up to 4 cm from the sapwood/heartwood boundary suggest the possibility that radial movement started to occur soon after Rb injection. The relocation continued at 20 days after the injection (Fig. 3), and would decline at a certain point of the time after the cease of Rb injection.

As mentioned above, radial movement of injected Rb caused by diffusion is likely to be limited. In addition, the low moisture content at white zone between sapwood and heartwood will hamper the diffusion of injected Rb to heartwood. The example of white zone hampering the dye diffusion in Japanese cedar is found in the study by Ohashi et al. [16]. They soaked freshly cut log of living Japanese cedar in 0.5% acid fuchsin aqueous solution overnight, and observed that the dye ascent mainly inner most sapwood. Since transpiration stream no longer flowed in the log, the movement of the dye was considered to be caused by diffusion. Color photos (e.g., Plate 1) in the report of Ohashi et al. [16] showed the dye did not go into the white zone. Other evidence indicating the white zone as a barrier

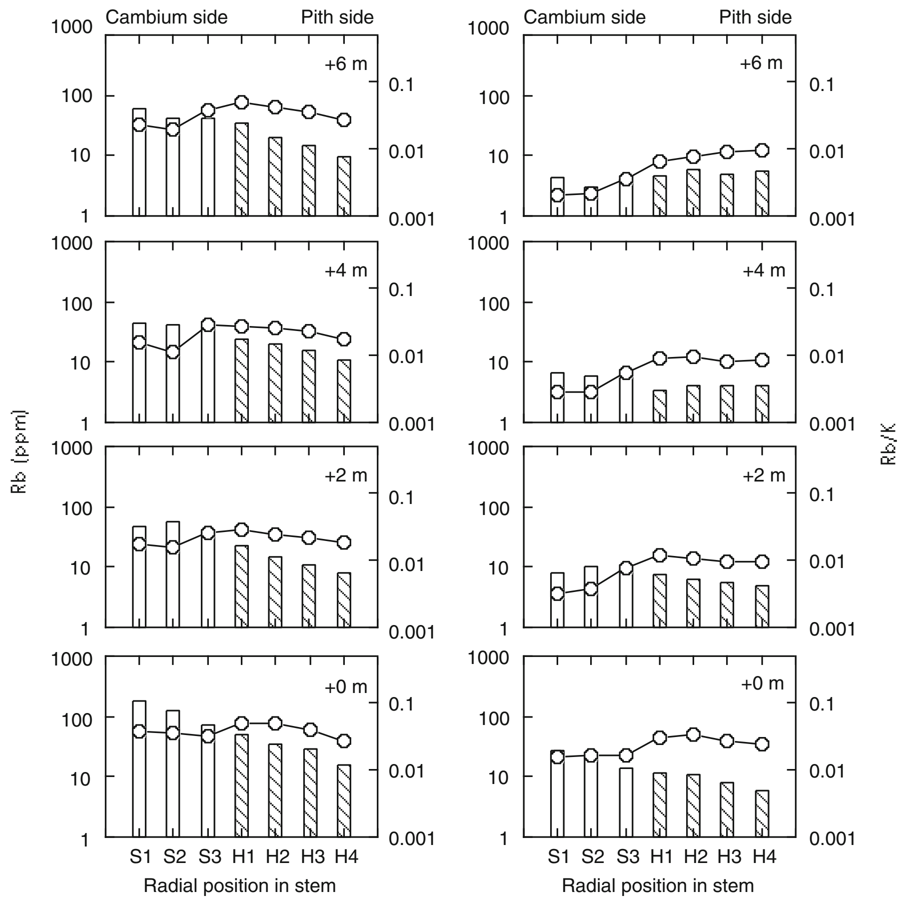


Fig. 4 Rb content and Rb/K in Rb-injected Kumotooshi cultivar at 172 days after the treatment. KT5 (*left*) and KT6 (*right*). Note that *vertical axes* are in logarithm. *Circles* Rb content, *white bars* Rb/K in sapwood, *gray bars* Rb/K in heartwood

of radial movement of minerals is found in an experiment studying transverse migration of minerals in green wood. In the experiment under a direct current (DC) potential by Minato et al. [14], they showed the distribution changes of trace elements in wood blocks, each of which was containing sapwood and heartwood of Japanese cedar. When they set the heartwood side as cathode under a 400 V of DC potential, K concentration in the portion nearest the cathode increased with time. However, the results (Fig. 3a in the article) indicated that K migration from sapwood to heartwood within the initial 30 min seemed to be less than expected. It was 2 h later in their experiment applying 400 DC volt to specimens that most of K in sapwood migrated to heartwood. The results indicate that even under a 400 DC volt K migration across the sapwood–heartwood boundary is still difficult. In our Rb injection experiment, there is no such driving force that promotes Rb migration to heartwood. Simple diffusion along the concentration gradient between sapwood and heartwood caused by Rb injection cannot be the driving force, because Rb content in the heartwood continued increasing even after Rb content in the sapwood became lower. Thus, we consider the increase of Rb in heartwood as active transport in Japanese cedar stem, and ray seems to be the only pathway connecting sapwood and heartwood. In fact, one photo explaining the longitudinal pathway of dye movement (Plate 9: Ohashi et al. [16]) also clearly shows that only ray is stained with dye in the sapwood, although the authors did not referred to that.

In heartwood region, Rb showed continuous movement even after cease of Rb injection as indicated in the different distribution patterns of Figs. 2 and 4. At the first 10 and 20 days after injection, Rb and Rb/K decrease monotonously from H1 to H4 in Figs. 2 and 3. At 172 days after injection, Rb content and Rb/K in heartwood decrease from H1 to H4 (Fig. 4) less remarkably than those at 10 and 20 days, suggesting that Rb movement from outer- to inner heartwood had continued after the cease of Rb injection. There is no living tissue in the heartwood, and hence no physiological control will function on the distribution of injected Rb. If the heartwood is assumed to be a homogenous organic material with ion exchange sites, the behavior of Rb ion is ruled by simple physicochemical process. Rubidium that has reached to the outer heartwood across the sapwood–heartwood boundary will diffuse in the heartwood according to the concentration gradient with repeating adsorption and desorption. The movement of Rb will cease at the adsorption/desorption equilibrium between sap and cell wall, at which point Rb concentration in the sap has to be homogenous. In fact, alkali metals in the sap in the heartwood of Japanese cedar are evenly distributed [17], although large variation of moisture distribution within heartwood is common for the species [18].

Seasonal difference in radial movement of Rb in the stem of Japanese cedar

Clear seasonal difference in radial movement of Rb is not observed between growing and resting periods of Japanese cedar. The radial distribution of Rb in the stem at 204 days after the injection at the beginning of September (our previous study [4]) is very similar to that in the present study at 172 days after the injection in mid May. This means injected Rb is transferred from the sapwood to the heartwood and then diffuses in the heartwood in both the resting and growing periods. Physiological difference between growing and resting periods of Japanese cedar has been reported for sapwood such as difference in moisture distribution [16], and in element content in sap [17], but no research has referred to seasonal physiological changes in heartwood as far as we know.

Our results also indicate that relocation of sapwood-injected Rb to the heartwood will proceed regardless of seasonality of heartwood formation. Heartwood formation of Japanese cedar in the warm-temperate zone starts from late summer to early autumn and stops in following spring [19]. In our results, Rb movement from sapwood to heartwood was observed in both active and non-active periods of heartwood formation. High concentration of alkali metals including Rb in the heartwood of Japanese cedar has been reported in connection with a certain physiological function in heartwood [9–11], but the phenomenon is not corresponding to the timing of cytological changes of ray parenchyma relating to heartwood formation. From this point of view, minerals in the heartwood of Japanese cedar have a relation not with the heartwood formation process but with a certain process maintaining the heartwood characteristics as discussing below.

Accumulation of K in the heartwood of Japanese cedar inferred from the movement of injected Rb

Since plants cannot effectively discriminate such ions that have similar chemical properties as K and Rb, and Ca and Sr at the cellular level, these ions are expected to tend to resemble each other in their long-distance translocation in the plant body [20]. This expectation is supported by some experiments, one of which reported that the ratio of radioactively labeled Rb to K was almost constant, regardless of their contents, through the parts of sugar cane [21]. Similar behavior of K and Rb is also reported in uptake via roots by rice plant [22] and tree seedlings [23], indicating validity of using Rb as an analog for K. Considering Rb as an analog of K, we discuss the accumulation of K in heartwood of Japanese cedar based on our results of Rb injection.

When and how is K accumulated in heartwood of Japanese cedar? Rb injection in present and previous [4] experiments suggests that while moving up in sapwood, K is transferred gradually and continuously to heartwood both in the growing and resting periods. The process of radial movement of K inferred from the results of Rb injection experiment is likely to be (1) active transport via ray parenchyma from sapwood to heartwood, and (2) diffusion in heartwood. Although the relocation seems to be closely related with heartwood formation, its timing is different from cytological changes of ray parenchyma accompanying heartwood formation.

It is still insufficient with present results to discuss why K and other alkali metals are accumulated in heartwood of Japanese cedar. However, because Japanese cedar, especially individuals with dark-colored heartwood, contains more amounts of alkali metals in its heartwood than many tree species, no doubt the high alkali metal content affects the characteristics of its heartwood. A recent investigation revealed that pH values of heartwood sap are very close between contrasted two cultivars, Kumotooshi with high moisture in heartwood and Boka with low moisture in heartwood (Fujimoto, unpublished data). In spite of the considerable difference in heartwood moisture (189 and 56%, respectively) and K content (2440 and 1740 ppm, respectively), the pH value was around 7.7 for both cultivars. This observation strongly suggests that pH of heartwood is genetically regulated by providing heartwood with cations of mainly K and other alkali metals. Morikawa et al. [5] have reported a similar observation for three Japanese cedar cultivars. Based on the similar point of view, Ohashi et al. [24] have investigated the buffer capacity of living stem of Japanese cedar on fresh and dry wood basis. They reported that the buffer capacity of living tissue generally decreased in the order of phloem, current-year formed xylem, heartwood, sapwood and white zone. Since buffer capacity means the degree of pH regulation function, it is appropriate to express in unit weight of solution. In the calculation by Ohashi et al. [24], the buffer capacity of heartwood is smaller than that of current-year xylem for a tree harvested in May (Tables 2 and 4 in Ohashi et al. [24]), but the former becomes greater than the latter when we convert the values into those in sap weight basis. It is noteworthy that heartwood without any living tissue has large buffer capacity in its sap compared with the current-year xylem with active living tissue. It has not yet clarified what substances are responsible for buffer capacity in heartwood sap, and what is the functional significance of buffer capacity. Some of heartwood polyphenols in Japanese cedar modify their structure under alkali condition to exhibit dark color [25], and K is one of the minerals responsible for the alkali condition [26]. If such heartwood polyphenols have some advantage such as anti-fungal effect, e.g., they are more effective when dissociated. Alkali metals as K in heartwood will function promoting the dissociation of polyphenols. In this context, large buffer capacity of heartwood substances is not for regulating pH. The low dissociation constant of heartwood substances requires something promoting dissociation, and alkali metal ions will meet the requirement. Further study should be focused on the mutual interaction between alkali metals and acidic compounds such as heartwood phenols in Japanese cedar.

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