

# Chapter 10

## Application of the Artificial Annual Environmental Cycle and Dormancy-Induced Suppression of Cesium Uptake in Poplar



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**Abstract** In perennial woody plants, dormancy-induced alteration of potassium (K) localization is assumed one of the mechanisms for adapting and surviving the severe winter environment. To establish if radio-caesium ( $^{137}\text{Cs}$ ) localization is also affected by dormancy initiation, the artificial annual environmental cycle was applied to the model tree poplar. Under the short day-length condition, the amount of  $^{137}\text{Cs}$  in shoots absorbed through the roots was drastically suppressed, but the amount of  $^{42}\text{K}$  was unchanged. Potassium uptake from the rhizosphere is mainly mediated by KUP/HAK/KT and CNGC transporters. However, in poplar, these genes were constantly expressed under the short-day condition and there were no up- or down-regulation. These results indicated the suppression of  $^{137}\text{Cs}$  uptake was triggered by the short-day length, however, the key transporter and the mechanism remains unclear. We hypothesized that Cs and K transport systems are separately regulated in poplar.

**Keywords** Artificial annual environmental cycle · Poplar · Dormancy · Uptake · Transporter

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## 10.1 Introduction

In 2011, radionuclides were released into the environment due to the Fukushima Daiichi Nuclear Power Plant accident. Among the released radionuclides, radio-caesium ( $^{137}\text{Cs}$ ) has been considered the main environmental contaminant. A large part of the contaminated land was forested and, after the accident, the  $^{137}\text{Cs}$  deposition to tree canopies, uptake through leaves and/or bark, and the translocation to growing branch were actively investigated (Kato et al. 2012; Takata 2013; Kanasashi et al. 2015). However,  $^{137}\text{Cs}$  uptake from the contaminated soil through the root was not well investigated because of methodological challenges. Therefore, the physiological knowledge of Cs transfer from the soil and its distribution among the tree organs is limited.

Cesium has a chemical property similar to potassium (K), but it is not an essential nutrient for plants. Generally, the rhizosphere Cs concentration (almost all is stable  $^{133}\text{Cs}$ ) is less than approx. 200  $\mu\text{M}$  and not toxic to plant growth (White and Broadley 2000). Cesium uptake and translocation within the plant body are considered to be mediated by  $\text{K}^+$  transport systems (White and Broadley 2000). *Arabidopsis* HAK5 (*AtHAK5*) is one of the best investigated root  $\text{K}^+$  uptake transporters, and its mutant, *athak5*, showed a tolerance against 300  $\mu\text{M}$  Cs treatment under low K conditions (Ahn et al. 2004; Gierth et al. 2005; Qi et al. 2008). *AtCNGCs* are Voltage-Independent Cation Channels (VICCs) type  $\text{K}^+$  permeable channels and *AtCNGC1* is the candidate gene for Cs uptake identified by quantitative trait locus analysis in *Arabidopsis* (Leng et al. 1999; Kanter et al. 2010).

To understand  $^{137}\text{Cs}$  behavior within woody plants, Cs content in each organ should be revealed under each seasonal environment, because K distribution among tree organs is changed by the seasonal transition. To combine the seasonal change of Cs distribution and the genetic information related to Cs transport, we used poplar as an experimental plant, although it is not the major tree species in the Fukushima region. Poplar is a perennial deciduous tree and the seasonal cycle of growth and dormancy is distinct. The genome of *Populus trichocarpa* is available (Tuskan et al. 2006) and the findings related to the Cs and K transport mechanisms obtained from crop research are applicable. Moreover, the high transfer rate of Cs from soil to poplar leaves has been observed under  $^{137}\text{Cs}$  contaminated regions in Europe (International Atomic Energy Agency (IAEA) 2010).

In trees, the phase shift from growth to dormancy is a basic winter adaptation mechanism (Jansson et al. 2010) and the transition of meristems into dormant buds is crucial for cold adaptation to protect the meristems against hazardous frosts. By perceiving the change in photoperiod and temperature, woody plants can shift their growth stage (Welling et al. 2002), and the initiation of cold acclimation under the short-day length increases endogenous abscisic acid levels and reduces endogenous gibberellic acid levels (Olsen et al. 1997; Welling et al. 1997; Mølmann et al. 2005). In beech (*Fagus sylvatica* L.), leaf K content is rapidly decreased before shedding and the retrieved K is deposited in the cortex and pith tissues of the stem (Eschrich et al. 1988). Japanese native poplar (*Populus maximowiczii*) can decrease leaf K

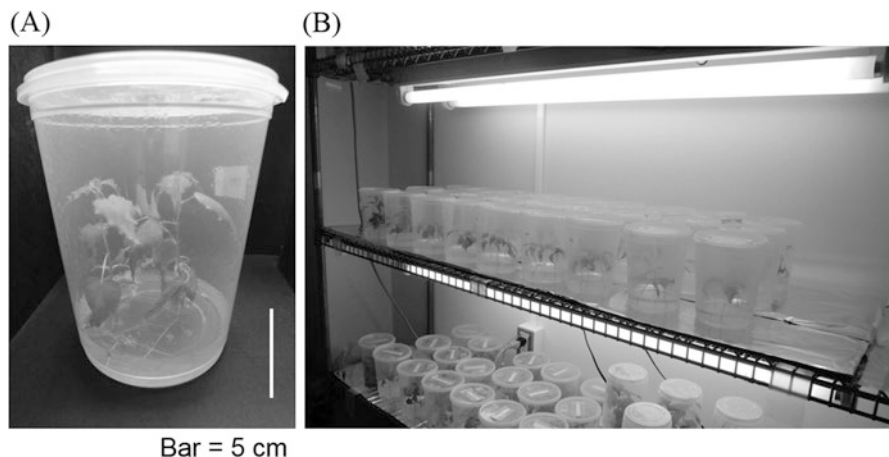
concentration after dormant bud formation (Furukawa et al. 2012). In addition, the increase of K concentration in xylem sap was observed during the winter period in field grown *Populus nigra* (Furukawa et al. 2011). These K behaviors implied the existence of a re-translocation mechanism and it is assumed that K and Cs are transported to K required organs for growth regulation and/or survival.

In this chapter, we will outline the experimental method of the artificial annual environmental cycle for cultivating small scale sterilized poplar and the investigation of  $^{137}\text{Cs}$  and  $^{42}\text{K}$  uptake through their roots under long and short photoperiod conditions.

## 10.2 Application of the Artificial Annual Environmental Cycle to Poplar

In poplar, dormancy is primarily initiated in response to short-day lengths (Sylvén 1940; Nitsch 1957), and the recent genetic and physiological understandings of dormancy initiation and break make poplar a highly suitable model tree for investigating growth rhythms. And the *Populus trichocarpa* genome was sequenced and expressed sequence tags of *Populus* were also identified (Kohler et al. 2003; Sterky et al. 2004). To utilize these advantages, we used poplar Hybrid aspen T89 (*Populus tremula x tremuloides*) as our experimental plants for investigating the shift of K and Cs distribution.

Hybrid aspen T89 were cultured in half-strength Murashige & Skoog (MS) medium in a sterilized container (height 14 cm, diameter 11 cm) (Fig. 10.1a) under light- and temperature-controlled conditions; 16 h light (light intensity



**Fig. 10.1** Growth condition of poplar. (a) The container for sterilized culture. The lid of the container has a microscopic pore air inlet. Bar = 5 cm. (b) Cultivation condition of artificial annual environmental cycle

**Table 10.1** Culture conditions in artificial annual environmental cycle

	Mimicked season	Kurita et al. 2014			Our condition		
		Temperature (°C)	Light/dark (h)	Cultivation period (week)	Temperature (°C)	Light/dark (h)	Cultivation period (week)
Stage-1	Spring/summer	25	14/10	4	23	16/8	3
Stage-2	Autumn	15	8/16	4	23	8/16	10
Stage-3	Winter	5	8/16	8–12	4	8/16	4

37.5  $\mu\text{mol m}^{-1} \text{s}^{-1}$ ) and 8 h dark cycle, 23 °C (Fig. 10.1b). Once a month, each plant was cut approx. 5 cm below the shoot apex and replanted in a container containing new MS medium under sterile conditions.

The annual cycle of poplar growth is re-created in the artificial annual environmental cycle, which is a modification of a similar method by Kurita et al. (2014). The poplar was treated with three stages: Stage-1 (Spring and Summer) 23 °C, 16 h light /8 h dark, Stage-2 (Autumn) 23 °C, 8 h light/16 h dark and Stage-3 (Winter) 4 °C, 8 h light/16 h dark (Table 10.1). Poplars can break its dormant bud after the return to Stage-1 within 2 weeks. In our artificial annual environmental cycle, in contrast to Kurita et al. (2014), the temperature in Stage-2 was set to 23 °C. Our preliminary experiments revealed that the dormant bud formation can be triggered by 4 weeks of short day-length treatment when the temperature is less than 23 °C. To minimize the environmental factors related to the dormancy initiation, the temperature was kept constant in Stage-1 and -2.

### 10.3 Measurement of $^{137}\text{Cs}$ and $^{42}\text{K}$ Distributions in Poplar

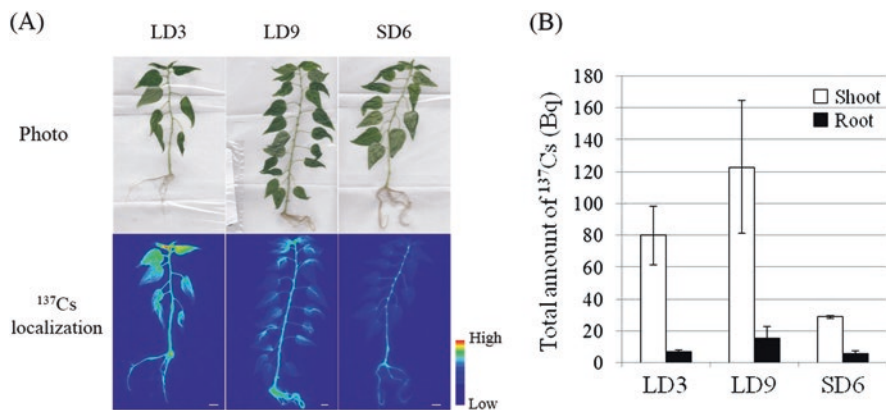
Under the artificial annual environmental cycle using *Populus alba* L., the shift of growth condition from Long Day (LD) to Short Day (SD) condition decreased the phosphate contents in lower leaves (Kurita et al. 2014). This change of phosphate content suggested the existence of a mechanism for the re-translocation of phosphate from lower leaves to younger upper leaves with seasonal changes. Regarding calcium (Ca) translocation, Furukawa et al. (2012) indicated the Ca transport from root to shoot is also regulated by the shift from LD to SD in *Populus maximowiczii*. To investigate if a similar shift occurs for  $^{137}\text{Cs}$ , Cs uptake through roots and its behavior within the plant body was compared in LD and SD conditions (Noda et al. 2016).

Poplars were grown under Stage-1 (LD) condition for 3 or 9 weeks (LD3 and LD9) in a light- and temperature-controlled environment. For investigating the effect of seasonal transition, a part of the LD3 plants were grown under Stage-2

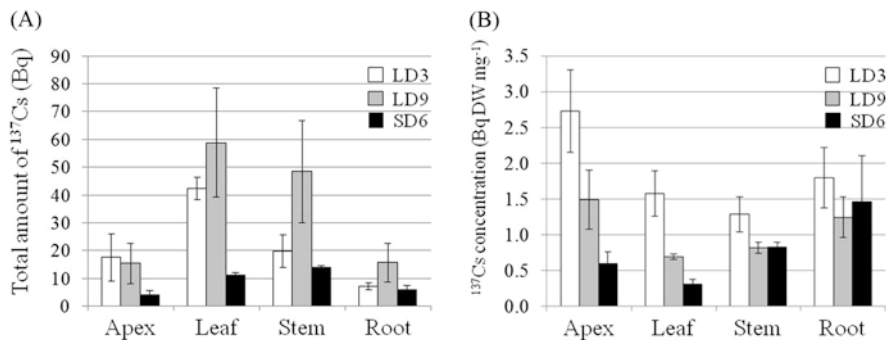
(SD) conditions for an additional 2, 4 and 6 weeks (SD2, SD4 and SD6). After those cultivations,  $^{137}\text{CsCl}$  (25 kBq, with  $0.1 \mu\text{M } ^{133}\text{CsCl}$ ) or  $^{42}\text{K}$  (8 kBq, with  $0.1 \mu\text{M } ^{39}\text{KCl}$ ) (Aramaki et al. 2015; Kobayashi et al. 2015) solution was added to the growth medium to observe root absorption. Cesium-137 distribution was investigated with the autoradiography technique in LD3, LD9 and SD6 plants and the harvested plants were cut into four parts, apex (shoot apex and top three leaves), leaf (remaining leaves and petioles), stem and root.

Figure 10.2a displays the localization of  $^{137}\text{Cs}$  through root absorption under LD3, LD9 and SD6 conditions. In LD3 plants,  $^{137}\text{Cs}$  was localized entirely and the radiation intensity around the apex was higher than other organs. Similarly, LD9 which was the same age as SD6 plants and grown under LD condition also showed the same  $^{137}\text{Cs}$  behavior as LD3 plants. In SD6 plants,  $^{137}\text{Cs}$  was mainly localized in the stem and root, furthermore, the total  $^{137}\text{Cs}$  quantity seemed to have decreased. Comparing  $^{137}\text{Cs}$  in the shoot (all shoot organs) and root under LD3, LD9 and SD6, the quantity of  $^{137}\text{Cs}$  in shoots under SD6 condition was the lowest (Fig. 10.2b). However,  $^{137}\text{Cs}$  quantity in roots was similar under each condition.

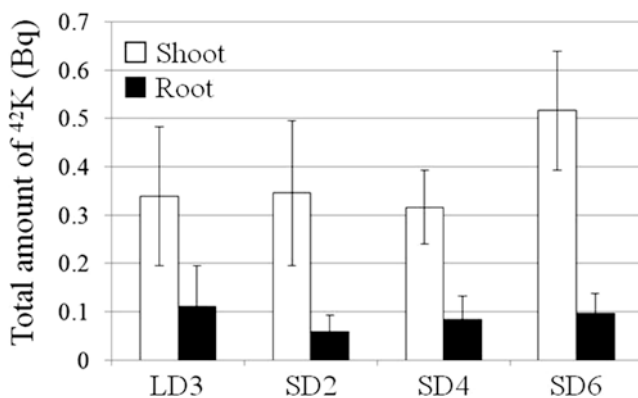
In respect to the amount of  $^{137}\text{Cs}$  in each organ,  $^{137}\text{Cs}$  mainly accumulated in leaves under LD3 condition (48.8% of applied  $^{137}\text{Cs}$ ) (Fig. 10.3a); in the LD9 condition, accumulation pattern was similar to LD3. However, under SD6 condition, leaf  $^{137}\text{Cs}$  content was the second highest (32.1%) and  $^{137}\text{Cs}$  mostly accumulated in the stem (39.7%). As for the  $^{137}\text{Cs}$  concentration, the effect of SD transition on  $^{137}\text{Cs}$  distribution mainly resulted in suppressing Cs transport into shoot apices and leaves (Fig. 10.3b).



**Fig. 10.2** Effect of short-day (SD) transition for  $^{137}\text{Cs}$  uptake activity in poplar. (a) Cesium-137 localization through root application under long-day (LD) conditions (LD3, LD9 and SD6). Upper images are photo and lower images indicate autoradiograph. Poplars were treated with  $^{137}\text{Cs}$  for 48 h. The color change from blue to red indicates  $^{137}\text{Cs}$  accumulation in autoradiography imaging. Bar = 1 cm. (b) Alteration of total amounts of  $^{137}\text{Cs}$  in poplar with SD transition. Poplars in each condition were treated with  $^{137}\text{Cs}$  for 48 h. Error bars represent standard deviation (n = 3). [Modified from Noda et al. (2016)]



**Fig. 10.3** Detailed  $^{137}\text{Cs}$  accumulation patterns under different growth condition. Poplars were separated into apices (including upper three leaves), leaves, stem and roots. (a) Detailed  $^{137}\text{Cs}$  accumulation in each organ after 48 h treatment under long-day (LD) and short-day conditions (SD) (LD3, LD9 and SD6). (b) Cesium-137 concentrations in each organ after 48 h treatment under LD3, LD9 and SD6 conditions. Three plants were tested for each condition. Error bars represent standard deviation (n = 3). [Modified from Noda et al. (2016)]



**Fig. 10.4** Effect of short-day (SD) transition for  $^{42}\text{K}$  uptake activity in poplar. Total amount of  $^{42}\text{K}$  in poplar shoot and root with SD transition.  $^{42}\text{K}$  under each condition was treated for 24 h. Three plants were tested for each condition. Error bars represent standard deviation (n = 3). (Modified from Noda et al. (2016))

From the result of  $^{137}\text{Cs}$  uptake assays, it was expected that the amount of  $^{42}\text{K}$  absorbed through the root was also down-regulated by SD transition. To explain the K uptake activity with seasonal change, poplar was treated with exogenous  $^{42}\text{K}$  application to the root and the quantity of K in shoot and root under LD3, SD2, SD4 and SD6 conditions were measured after 24 h incubation (Fig. 10.4). Contrary to our expectations, there was no difference in the amount of  $^{42}\text{K}$  in either root or shoot among the four conditions. These data suggest that the K demand for the rhizosphere was not changed by SD transition in poplar up to 6 weeks.

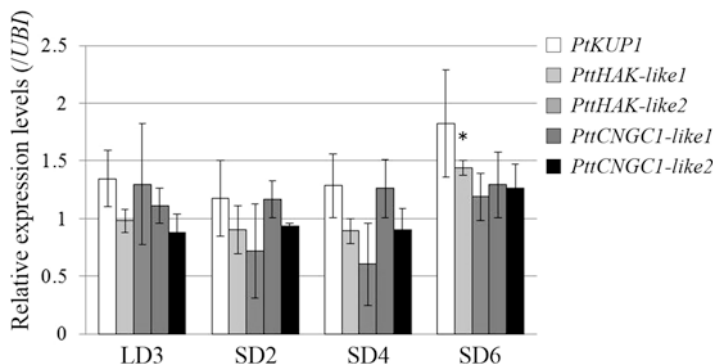
Comparing the data presented in Figs. 10.2 and 10.4,  $^{137}\text{Cs}$  accumulation decreased under SD6 condition but  $^{42}\text{K}$  accumulation remained constant through the SD transition. This inconsistency suggests that Cs accumulation might be separately controlled, and not part of the major K uptake systems in poplar. In addition, it is also implied that the responsible transporter for poplar Cs uptake might be poorly involved in K uptake because no decrease of K accumulation was observed under the low Cs accumulation condition.

## 10.4 Expression of Potassium Influx Transporters in Poplar Root

To identify the Cs uptake responsible transporter, we investigated the expression patterns of some candidate genes under SD condition. Among various  $\text{K}^+$  uptake transporters, we focused on high-affinity  $\text{K}^+$  transporters, KUP/HAK/KT family (Rubio et al. 2000; Mäser et al. 2001; Gupta et al. 2008), and low-affinity channel, cyclic-nucleotide-gated channel (CNGC) (Hua et al. 2003; Harada and Leigh 2006; Ahmad and Maathuis 2014). As for one of the KUP/HAK/KT family genes, we focused on *Populus tremula*  $\text{K}^+$  uptake transporter 1, *PtKUP1* (POPTR\_0003s13370), identified from hybrid aspen. *PtKUP1* was used for the complementation test using K uptake-deficient *E. coli* mutant. The addition of toxic level Cs to the culture media inhibited the growth of *E. coli* expressing *PtKUP1* strongly, suggesting *PtKUP1* can transport both K and Cs (Langer et al. 2002). In addition to *PtKUP1*, there are eight *AtHAK5* orthologue genes in *Populus trichocarpa*. Arabidopsis *HAK5* (*AtHAK5*) is a well-known root  $\text{K}^+$  uptake transporter and it has been reported that the induction of *AtHAK5* is enhanced by  $\text{K}^+$  deficiency (Ahn et al. 2004; Gierth et al. 2005) or by  $\text{Cs}^+$  applications when there is sufficient  $\text{K}^+$  (Adams et al. 2013). Based on the similarity of those nine putative KUP/HAK/KT family  $\text{K}^+$  transporters, POPTR\_0010s10450 and POPTR\_0001s00580 were chosen as highly homologous genes with *AtHAK5*. We identified POPTR\_0010s10450 and POPTR\_0001s00580 homologues in hybrid aspen T89 and named those *Populus tremula x tremuloides* *HAK-like1* (*PttHAK-like1*) and *PttHAK-like2*, respectively. Similar to *HAK-like* genes, two *CNGC-like* genes were selected from nine *AtCNGC1* homologue genes in *P. trichocarpa*. POPTR\_0012s01690 and POPTR\_0015s02090 had a higher similarity to *AtCNGC1* and those homologues in hybrid aspen T89 were named *PttCNGC1-like1* and *PttCNGC1-like2*, respectively.

The expression patterns of these genes were measured during the transition to the SD condition (Fig. 10.5). There was no significant change in *PtKUP1* expression. *PttHAK-like1* showed steady expression until SD4 condition and was slightly up-regulated by about 1.5-fold under SD6 condition. *PttHAK-like2* exhibited the decreasing tendency in SD2 and SD4 plants, but remained statistically constant through the SD transition. Two *PttCNGC1-like* genes also expressed relatively constantly under SD condition.





**Fig. 10.5** Effect of short-day (SD) transition on transcriptional expression of *HAK* and *CNGC* orthologue genes in poplar root. Total RNA was isolated from root and these gene transcript levels were analyzed by qRT-PCR. *UBIQUITIN* was used as the reference gene. All gene expression levels were normalized by expression level of LD3 condition. Error bars represent standard deviation. \* indicated significant difference to the level of LD3 expression level (\* < 0.01). (Modified from Noda et al. (2016))

In this experimental condition, dormant buds were formed up to 4 weeks after starting the short-day treatment and, therefore, the re-translocation of K should have already commenced at SD6. However, the results showed that the  $^{42}\text{K}$  accumulation through root uptake and gene expression related to the root K uptake were almost constant. Steady-state of K requirement under SD condition seems to indicate abundant K was stored in the plant body and the change of K demand might be covered by the internal re-translocation.

## 10.5 Perspectives in $\text{Cs}^+$ Transporter Research

Despite the constant K accumulation patterns under SD conditions, Cs accumulation was drastically decreased in SD6 plant (Figs. 10.2 and 10.4). Cesium uptake and translocation is considered to be regulated by plant K transport system, however, no down-regulation in candidate genes was observed at SD6 (Fig. 10.5). However, it is not known if elemental transport is only regulated by gene expression and not by protein activity (White and Broadley 2000). But the inconsistency of  $^{42}\text{K}^+$  and  $^{137}\text{Cs}^+$  localization patterns indicates a possible existence of an unknown Cs uptake system which preferentially transports Cs rather than K.

Based on our experimental design to identify permeable Cs transporters, it would appear that the mechanisms regulating the specificity of these transporters are very complex and it might be difficult to identify the responsible genes through reverse genetics. Our studies have also demonstrated that Cs uptake in poplar is regulated by the photoperiod, therefore, the mechanisms of the dormancy initiation might be involved in the suppression of Cs uptake. Using our data and the increasing



knowledge of dormancy, the mechanisms of Cs uptake from contaminated soil to forest trees should be revealed and we hope that the understanding of Cs circulation within the forest ecosystem will be utilized in the prediction of Cs transfer among the terrestrial environment in the near future.

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