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Seed Dormancy and Germination of *Scrophularia koraiensis*, an Endemic Species in the Korean Peninsula

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Abstract

This study aimed to develop seed-based mass propagation techniques for the conservation and horticultural and medicinal uses of *Scrophularia koraiensis* Nakai, an endemic plant in the Korean Peninsula. Seeds were collected from four different locations (accessions) and subjected to untreated (control), gibberellic acid (GA)-only treatment, cold stratification-only treatment, or a cold stratification + GA treatment. Except for seeds collected from one location, the control group exhibited low germination of below 20% in all other locations. However, the GA-only and cold stratification-only treatments released seed dormancy and promoted germination compared with the control. In particular, the cold stratification-only treatment at 5 °C for 4 weeks resulted in about 80% germination in all accessions and demonstrated positive effects on germination speed and uniformity. These findings indicated that *S. koraiensis* seeds exhibit non-deep physiological dormancy (PD). Upon comparing the seed dormancy classes across various species of *Scrophularia*, native to different continents and countries, we confirmed that PD is very well conserved in the genus *Scrophularia*. Therefore, the study outcomes will provide fundamental and practical insights into the seed dormancy and germination characteristics of various *Scrophularia* species for future studies.

Keywords: native plants; physiological dormancy; seed propagation; trait stasis

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1. Introduction

Scrophularia L., belonging to the family Scrophulariaceae and tribe Scrophularia, comprises about 270 taxa. They are predominantly distributed in the temperate regions of the Northern Hemisphere, with a few species found in the Southern Hemisphere [1–4]. In Eastern cultures such as China and Korea, the roots of *Scrophularia* plants have been used as anti-inflammatory, antipyretic, and detoxifying herbal medicines [5,6]. In Korea, *S. buergeriana* Miq. is considered the original plant of *Scrophularia* radix (Hyun-Sam), a herbal

medicine also known as Korean Hyun-Sam [7]; additionally, *S. kakudensis* Franch., *S. koraiensis* Nakai, and *S. takesimensis* Nakai are used as alternatives to this herbal medicine [8,9].

Reports suggest that plants belonging to the genus *Scrophularia* L., which is native to the Korean Peninsula, are classified into six species and one variety (seven taxa). This classification is based on external morphology such as flowering time; growth traits of inflorescence, peduncle, floret, calyx, stem, and leaf; characteristics of root and seed; and internal transcribed spacer (ITS) DNA sequence data [4,10,11]. Among them, three species, including *S. koraiensis* Nakai, *S. cephalantha* Nakai, and *S. takesimensis* Nakai, were reported to be endemic only to the Korean Peninsula in East Asia [12,13].

S. koraiensis is a perennial herb growing in the semi-shade of mountainous areas, reaching a height of approximately 1.5 m, and flowering in the month of July. Glandular trichomes develop throughout the plant during the early growth period but nearly disappear by the flowering period [4]. Its fruit is an ovoid capsule that matures from August to September. Recent studies have shown the preventive effects of *S. koraiensis* on bone disorders, particularly through inhibiting osteoclast differentiation and bone resorption [9]; additionally, its extracts could be used as a potential therapeutic agent for allergic airway inflammation [14]. As a member of the family Scrophulariaceae, *S. koraiensisis* has been designated as a "biological resource subject to approval for overseas export" in Korea. This designation reflects the high protection value of these plants for biodiversity conservation, thereby requiring approval from the Minister of Environment in accordance with the provisions of the Ministry of Environment Ordinance while exporting them [15]. Additionally, *S. koraiensisis* has been identified as a target plant to monitor mid- to long-term adaptability of plant resources to climate change on the Korean Peninsula [16]. Therefore, developing mass propagation technologies is essential for the sustainable conservation and utilization of this plant; however, research in this area remains limited.

Seed-based mass propagation of plants is essential for preserving genetic diversity and promoting its sustainable use. Studies have reported characteristics of seed germination for several *Scrophularia* plants. When seeds were treated with 400 ppm GA_3 for 24 h, the seeds of *S. striata*, a naturally growing plant in the western parts of Iran, showed the best germination [17]. When seeds were soaked in 200 mgL^{-1} GA_3 for 24 h, the seeds of *S. takesimensis*, a plant native to the Korean Peninsula, exhibited approximately 80% germination [18]. The seeds of *S. marilandica*, a plant native to Canada, exhibited nearly complete germination following treatment with 3×10^{-4} M GA_3 [19]. However, there are no reports on the seed propagation of *S. koraiensis*. We hypothesized that GA treatment would break dormancy in *S. koraiensis* seeds, as reported for other *Scrophularia* species. Given the known interaction between GA and cold stratification [17,19], additional experiments were conducted to examine this relationship. Therefore, this study aimed to improve the seed propagation efforts by determining whether seed dormancy is present in *S. koraiensisis* seeds and, if so, identifying its type. In particular, (1) the water imbibition of seeds; (2) the morphology of seeds and embryo; and (3) the effects of cold stratification, gibberellic acid (GA) treatment, and seed collection sites were investigated.

2. Materials and Methods

2.1. Seed Collection

The seeds investigated in this study were collected between 2 and 4 September 2014 from *S. koraiensis* Nakai growing on Mt. Gariwang (Kari, Figure 1), Balwang (Balw), Gyebang (Gyeb), and Deokhang (Deok) in the Gangwon Province, Republic of Korea. Fully mature fruits were collected and brought to the laboratory, and only fresh seeds were selected for experiments. The fresh seeds were dried for 2 weeks and then refrigerated

at 5 °C for 6 months (WIM-RL4, Daihan Scientific Co., Wonju, Republic of Korea) until further use.



Figure 1. *Scrophularia koraiensis* inhabiting Mt. Kariwang, Gangwon Province, Republic of Korea.

2.2. Seed Water Absorption

The degree of moisture absorption of seeds was determined by placing the seeds in Petri dishes (90 × 15 mm), lined with two sheets of filter paper (Whatman No. 1, GE Healthcare, Buckinghamshire, UK) and containing at least 10 mL distilled water. Thereafter, the weight of the seeds was measured at room temperature (22–25 °C) at predetermined time intervals of 0, 2, 4, 8, 12, 24, and 48 h. The moisture on the surface of the seeds was wiped off with a tissue, and the weight of 40 seeds was measured at each time point in triplicate. The increase in the mass of the seeds was calculated using the following formula:

$$\%Ws = [(Wh - Wi)/Wi] \times 100$$

Here, Ws denotes the increase in the mass of the seeds; Wh refers to the mass of seeds measured after imbibition at a specific time point; and Wi indicates the initial mass of the seeds.

2.3. Seed Germination

The seeds were collected from four different habitats, stored for 6 months at 5 °C and tested in four treatment groups: (1) no treatment (control), (2) GA-only treatment, (3) cold stratification-only treatment, and (4) cold stratification + GA treatment. For the GA-only treatment, seeds were soaked in a solution containing 800 mg·L^{-1} GA_3 for 24 h at room temperature (22–25 °C) prior to sowing. For the cold stratification-only treatment, seeds were placed in Petri dishes (90 × 15 mm) lined with two sheets of filter paper (Whatman No. 1, GE Healthcare, Buckinghamshire, UK) and containing 5 mL distilled water. To prevent moisture evaporation from the Petri dishes, the Petri dishes was sealed with parafilm, and additional distilled water was supplied when moisture was insufficient. The seeds were then incubated in a cold lab chamber (WIM-RL4, Daihan Scientific Co., Wonju, Republic of Korea) at 5 °C for 4 weeks of cold stratification before sowing. For the cold stratification + GA treatment, the seeds were first cold stratified using the same

method and then soaked in the GA solution for 24 h prior to sowing. For the control group, untreated seeds were sown.

Treated seeds of the three groups were sown, one seed per hole, in 128-hole plug trays (27.5 × 54.0 × 5.0 cm), which was filled with horticultural soil (TKS-2, Floragard, Oldenburg, Germany). These plug trays were placed in an experimental greenhouse at the Useful Plant Resources Center of the Korea National Arboretum in Yangpyeong-gun, Gyeonggi-do, Republic of Korea. The average temperature in the greenhouse was 18 ± 3.5 °C, and the natural day length was maintained without any artificial control. All experimental treatments were performed with 40 seeds in triplicate.

2.4. Data Collection and Statistical Analysis

Following each experimental treatment, germinated seeds were counted daily for 4 weeks, and germination percentage (GP), days to 50% of germination of final GPs (T_{50}), mean germination time (MGT), germination uniformity (GU), and germination speed (GS) were calculated using the following equations [20–22]. Germination was considered to have occurred when the radicle protruded through the seed coat and reached a length of approximately 1 mm.

$$GP = (N/S) \times 100$$

$$T_{50} = Ti + (Tj - Ti) \times (N/2 - Ni)/(Nj - Ni)$$

$$MGT = \sum(Tx \cdot Nx)/N$$

$$GU = \sum[(MGT - Tx)^2 \cdot Nx]/N - 1$$

$$GS = \sum(Nx/Tx)$$

Here, N represents the total number of seeds germinated; S denotes the total number of seeds tested; Ni refers to the total number of seeds germinated just before 50% germination for N was reached; Nj denotes the total number of seeds germinated just after 50% germination for N was reached; Ti refers to the germination period until Ni; Tj indicates the germination period until Nj; Nx is the number of seeds germinated on the day of irradiation; and Tx represents the number of days after irradiation.

The initial seed morphology and changes during the germination process were observed using a USB microscope (AM 3111 Dino-Lite premier, AnMo Electronics Co., New Taipei City, Taiwan) at 50–60× magnification.

Statistical analyses were performed using SPSS version 12 (SPSS Inc., Chicago, IL, USA), and ANOVA was performed to analyze the results of each treatment group and the interactions among factors including habitat and treatment strategies, particularly the cold stratification-only treatment and the GA-only treatment. Duncan's multiple range test ($p < 0.05$) was also used as a post hoc test to compare treatment means. Graphs were created using SigmaPlot 10.0 (SPSS Inc., Chicago, IL, USA).

3. Results

3.1. Seed Water Absorption

The seeds of *S. koraiensis* Nakai exhibited rapid water intake, reaching 84% of their initial mass within 3 h and exceeding 100% by 6 h, after which the hydration level remained constant for up to 48 h.

3.2. ANOVA Analysis of Germination Percentage

We observed that the cold stratification-only and the GA-only treatments significantly affected the germination process of *S. koraiensis* Nakai seeds ($p < 0.001$, Table 1). However, the effect of the seed collection location (habitat) was not statistically significant ($p = 0.0767$).

Additionally, the interactions of the treatment type and habitat, except the interaction of the cold stratification-only treatment and habitat, significantly affected the germination process.

Table 1. Three-way ANOVA (degrees of freedom, d.f., sum of squares, SS, mean square, MS, and level of significance, *p*-value) of the effects of habitat, cold stratification-only treatment, gibberellic acid (GA)-only treatment, and their interactions on the germination process of *Scrophularia koraiensis*.

Source of Variation	d.f.	SS	MS	F-Value	*p*-Value
Habitat (H)	3	451.31300	150.43767	2.51	0.0767
Cold stratification-only treatment (C)	1	27,174.04893	27,174.04893	452.62	<0.0001
GA-only treatment (G)	1	5879.71999	5879.71999	97.94	<0.0001
H × C	3	318.32682	106.10894	1.77	0.1732
H × G	3	1050.27104	350.09035	5.83	0.0027
C × G	1	6216.43873	6216.43873	103.54	<0.0001
H × C × G	3	823.85336	274.61779	4.57	0.0089

3.3. Germination Percentage (GP)

For seeds collected from Mt. Gariwang, we recorded 11.7% germination in the control group; however, germination increased to 70.7% and 93.6% in the GA-only and cold stratification-only treatment groups, respectively. The GP was 84.4% for the cold stratification + GA treatment group (Figure 2). For seeds collected from Mt. Balwang, we observed an 8.5% GP in the control group that increased to 65.8% and 89.3% in the GA-only and cold stratification-only treatment groups, respectively. The GP was 92.2% in the cold stratification + GA treatment group. For seeds collected from Mt. Gyebang, we recorded a 35.3% GP in the control group, 57.2% in the GA-only treatment group, and 90.4% in the cold stratification-only treatment group. The GP was 81% for the cold stratification + GA treatment group. For seeds collected from Mt. Deokhang, we observed a 12.8% GP in the control group that increased to 54.0% and 76.3% in the GA-only and cold stratification-only treatment groups, respectively. The GP was 89.4% for the cold stratification + GA treatment group. The seeds of *S. koraiensis* Nakai exhibited fully developed embryos at the time of maturation, and the germinated seeds subsequently formed normal cotyledons (Figure 3).

3.4. Germination Parameters

We observed a statistically significant effect of the cold stratification-only treatment on the germination parameters including MGT, GU, GS, and T_{50} (Table 2). However, the effect of the GA-only treatment was only statistically significant for GS. Additionally, the interaction between the two factors was statistically significant for all parameters except for GU.

Table 2. Effects of habitats, cold stratification-only treatment, and GA-only treatment on mean germination time (MGT), germination uniformity (GU), germination speed (GS), and days to 50% of germination (T_{50}) in *Scrophularia koraiensis* seeds.

Cold Stratification (A)	GA_3 (mg·L^{-1}) (B)	MGT	GU	GS	T_{50}
		Mt. Kariwang			
Control	0	16.99 a [1]	9.12 a	0.30 d	13.33 a
	800	14.53 b	11.17 a	2.15 c	10.01 b
4 weeks	0	9.63 d	2.67 b	4.26 a	7.00 c
	800	11.28 c	1.10 b	3.21 b	10.03 b

Table 2. *Cont.*

Cold Stratification (A)	GA_3 (mg·L^{-1}) (B)	MGT	GU	GS	T_{50}
		Mt. Barwang			
Control	0	15.73 a	7.96 a	0.24 c	13.83 a
	800	13.97 b	8.73 a	2.11 b	9.77 b
4 weeks	0	9.30 d	3.24 ab	4.23 a	3.90 c
	800	11.28 c	0.77 b	3.50 a	10.03 b
		Mt. Gyebang			
Control	0	18.21 a	9.23 a	0.86 d	14.60 a
	800	15.86 b	9.07 a	1.59 c	10.79 b
4 weeks	0	9.96 c	3.77 ab	3.99 a	6.76 c
	800	11.28 c	0.43 b	3.05 b	10.03 b
		Mt. Deokhang			
Control	0	16.36 a	8.09 a	0.34 c	13.39 a
	800	16.20 a	5.27 b	1.45 b	12.89 a
4 weeks	0	9.99 c	4.60 b	3.39 a	6.48 c
	800	11.29 b	0.84 c	3.38 a	10.03 b
F-test	A	407.660 **	31.617 **	391.701 **	169.242 **
	B	NS	NS	7.914 **	NS
	A × B	36.242 **	NS	67.596 **	107.895 **

[1] Mean separation was determined by Duncan's multiple range test at $p < 0.05$, with NS and ** indicating nonsignificant and significant differences at $p < 0.01$, respectively.

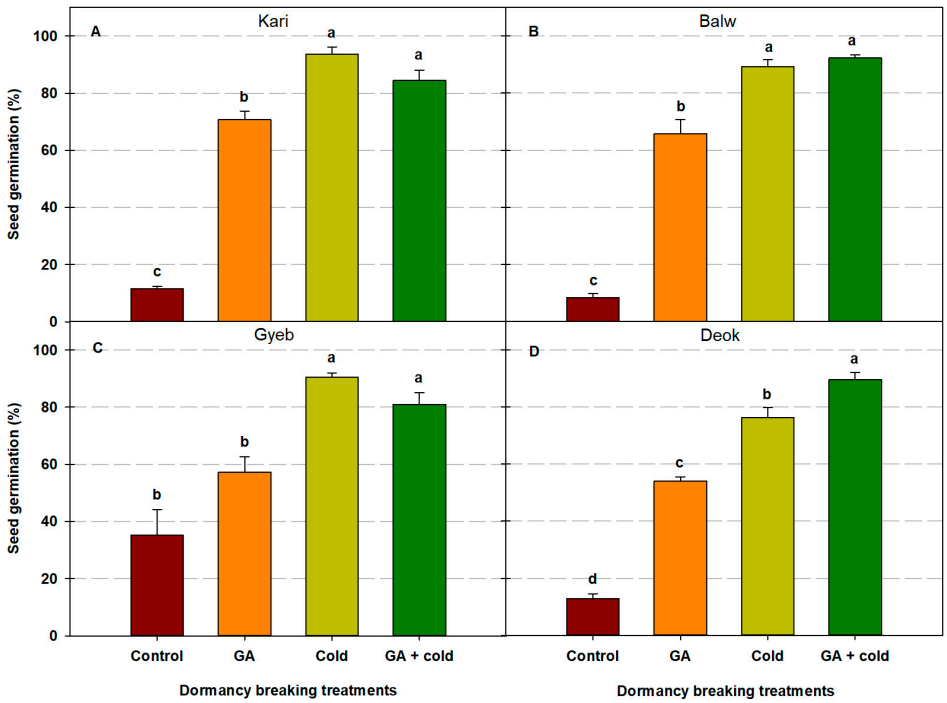


Figure 2. Effects of seed collection location, gibberellic acid (GA)-only treatment, cold stratification-only treatment, and cold stratification + GA treatment on the seed germination of *Scrophularia koraiensis*. The seeds collected from Mt. Gariwang (Kari) (**A**), Balwang (Balw) (**B**), Gyebang (Gyeb) (**C**), and Deokhang (Deok) (**D**) in the Gangwon Province, Republic of Korea, were used for this experiment. Forty seeds were assessed in triplicate. Different letters indicate significant differences based on Duncan's multiple range test ($p < 0.05$).

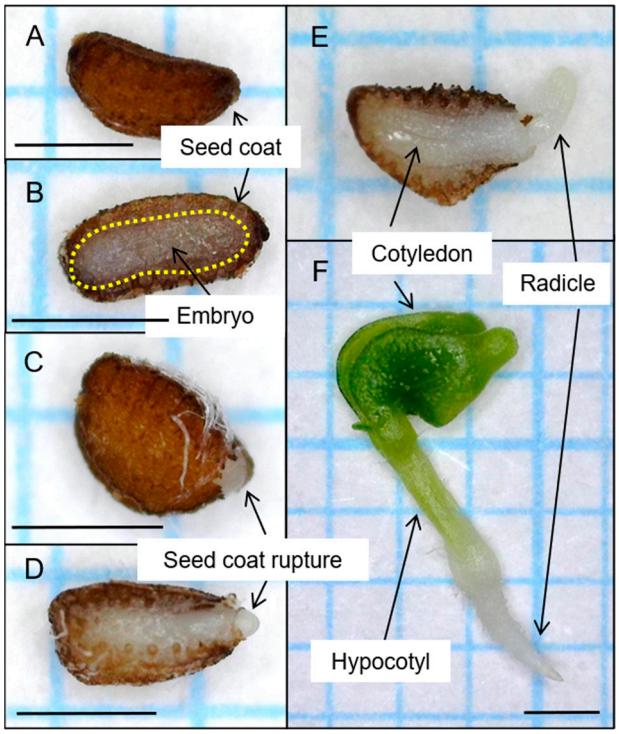


Figure 3. Morphology, germination, and seedling growth of *Scrophularia koraiensis* seeds. (**A**) Intact seed. (**B**) Fully developed embryo. (**C**,**D**) Seed coat rupture. (**E**) Germination. (**F**) Seedling. Scale bar indicates 1 cm.

4. Discussion

Seeds collected from Mt. Gyebang exhibited germination percentage (GP) of 35.3%, while seeds collected from the remaining three regions exhibited GPs below 20% (Figure 2). The Nikolaeva–Baskin seed dormancy classification system classifies dormancy into the following five types: physiological dormancy (PD), morphological dormancy (MD), morphophysiological dormancy (MPD), physical dormancy (PY), and combined dormancy (PY + PD) [23–25]. The seeds collected from all four regions had fully developed embryos at the time of detachment from the mother plant (Figure 3). Furthermore, fresh seeds absorbed more than 100% of their initial weight. These observations suggest that seed dormancy in *S. koraiensis* seeds is neither MD nor MPD, owing to the underdeveloped embryos, nor PY nor PY + PD, due to the impermeability of the seed coat. Instead, the results indicate that the seeds of this plant exhibit PD.

Based on the depth of PD, it has three levels, namely, non-deep, intermediate, and deep [26]. Cold (days or up to several months) or warm stratification can release the non-deep PD in seeds; additionally, reports suggest the potential of the GA-only treatment in effectively breaking seed dormancy [24,26]. Consequently, we used the cold stratification-only and GA-only treatments to break seed dormancy, which promoted germination in seeds collected from all four regions. However, for seeds collected from three regions excluding Mt. Deokhang, we observed no difference in the GP between the cold stratification-only and cold stratification + GA treatments. Therefore, the cold stratification-only treatment could sufficiently break seed dormancy, and the additional GA treatment proved unnecessary. Furthermore, the outcomes suggest the dormancy type of *S. koraiensis* seeds as non-deep PD. Reports suggest that dry after-ripening (DAR) positively affects breaking seed dormancy in plants with a non-deep PD, which includes seeds of *Osteomeles schwerinae* [27], *Primula poissonii* [28], *Rhodiola crenulate* [29], *Rheum nobile* [30], *Lamiophlomis rotata*, and *Marmoritis complanatum* [31], where DAR helped in reducing the depth of PD

and facilitated seed germination. In this study, seeds that had been dried and stored at 5 °C for 6 months after seed collection were used. Therefore, further research is essential to determine the dormancy-breaking effect of DAR treatment on *S. koraiensis* seeds.

Upon summarizing the outcomes of previous studies on the genus *Scrophularia*, Baskin and Baskin [24] reported that the seeds of *S. glabrata*, *S. incisa*, *S. marilandica*, *S. nodosa*, and *S. glabrata* exhibit PD. Additionally, seeds of *S. takesimensis*, native to the Korean Peninsula [18], and *S. stricta*, native to Iran [17], also reported to demonstrate PD. The outcomes of the present study also indicated that *S. koraiensis* seeds exhibit PD, thereby aligning with the previous studies and indicating that PD is well conserved in plants belonging to the genus *Scrophularia*. The phenomenon in which ecological and physiological characteristics, such as seed dormancy, remain conserved or exhibit little change despite plants of the same genus being distributed across different continents and long-term geographically separation is referred to as "trait stasis". In contrast, when these characteristics change gradually over geologically timescales as plants adapt to new habitats, including changes in seed dormancy and germination requirements, is known as "trait divergence (adaptation)" [32–34]. Accordingly, the findings of this study suggest that plants belonging to the genus *Scrophularia* may represent a case of "trait stasis" with respect to seed dormancy/germination.

In this experiment, the GA-only and cold stratification-only treatments effectively inhibited seed dormancy and promoted germination; however, the latter proved to be more effective (Figure 2). Adding GA treatment to the cold stratification-only treatment did not further promote germination. In contrast, adding cold stratification treatment to the GA-only treatment further promoted germination. Additionally, the cold stratification-only treatment demonstrated a positive effect on germination parameters, including MGT, GU, GS, and T_{50}, in seeds collected from all four sites (Table 2). Previous studies conducted in *S. striata* [17], *S. takesimensis* [18], and *S. marilandica* [19] also report similar germination-promoting effect through the cold stratification-only or GA-only treatments. For seeds with PD, factors including the content, synthesis, and sensitivity of plant hormones GA and ABA considerably affect the breaking of seed dormancy and promotion of germination. The sensitivity of the seeds to GA increases with the progressive release of non-deep PD. Additionally, a decrease in the sensitivity of ABA influences the transition of seeds from a dormant to a nondormant state [35,36]. This implies that the cold stratification-only treatment in the present study affected the content of GA and ABA, along with their sensitivity. While exogenous application of IAA alone does not significantly affect seed germination in a wild-type *Arabidopsis* species, its co-application with ABA markedly inhibits germination, suggesting that ABA may suppress seed germination through the auxin signaling pathway [37,38]. Seed germination is regulated by the formation of an endogenous indole-3-acetic acid (IAA) gradient; therefore, exogenous application of IAA does not significantly affect the germination process. Considerable research has been devoted to understanding the effects of after-ripening and low-temperature stratification treatments among the various types of seed dormancy, with particular emphasis on elucidating the molecular mechanisms underlying physiological dormancy (PD) [39–41]. Additional research is necessary to clarify the molecular mechanisms of diverse nondeep PD types in seeds.

5. Conclusions

The primary aim of our research was to develop a seed-based mass propagation technique for breaking seed dormancy and promoting germination in *S. koraiensisis* seeds. The results indicated that the cold stratification-only treatment at 5 °C for 4 weeks or immersion in 800 $mg \cdot L^{-1}$ GA_3 for 24 h effectively inhibited seed dormancy and increased germination. In particular, the cold stratification-only treatment exhibited positive effects across

seeds collected from four different locations, suggesting the relevance of the technique regardless of the collection location. The findings of this study suggest that *S. koraiensis* seeds possess non-deep PD. Furthermore, the study demonstrated that PD is highly conserved in *Scrophularia* species, native to various regions worldwide. Consequently, the cold stratification-only treatment can be consistently applied in future seed research and for practical mass propagation of plants within the genus *Scrophularia*.

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