

Article

Seed Dormancy and Germination Characteristics in Six *Solanum* Species Distributed on the Korean Peninsula

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Abstract

Crop wild relatives (CWRs) are critical resources for crop improvement and addressing food security. The genus *Solanum* includes many wild species genetically related to major crops. However, seed propagation methods for *Solanum* taxa distributed on the Korean Peninsula are not well-established. In this study, seed morphology and effects of incubation conditions on germination and dormancy were evaluated in 6 *Solanum* species classified as CWRs in Korea: *Solanum lyratum*, *S. japonense*, *S. nigrum*, *S. sarrachoides*, *S. americanum*, and *S. viarum*. The seeds possessed fully developed embryos at the time of dispersal and the seed coats readily absorbed water. We investigated germination characteristics under various temperatures, cold stratification periods, and gibberellic acid (GA₃) concentrations. Germination percentage of *S. lyratum* and *S. japonense* was significantly higher under cold stratification ($\geq 62.0\%$ after 12 weeks at 5 °C) or GA₃ treatment ($\geq 77.0\%$ at 1000 mg·L⁻¹) than for temperature treatment alone ($\leq 3.0\%$ at 25/15 °C), indicating non-deep physiological dormancy (PD). Seeds of *S. nigrum*, *S. americanum*, and *S. viarum* exhibited non-deep PD with conditional dormancy and higher germination efficiencies through GA₃ 1000 mg·L⁻¹ than under temperature treatment alone (25/15 °C). Seeds of *S. sarrachoides* were classified as non-dormant. These findings may contribute to the practical mass propagation of *Solanum*.

Keywords: *Solanum* species; crop wild relatives; seed dormancy; cold stratification; gibberellic acid; physiological dormancy; conditional dormancy



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1. Introduction

Interest in wild plants has increased, and the utilization and conservation of crop wild relatives (CWRs) are active areas of research [1–6]. CWRs are wild plants that are closely related to crops and regarded as the wild ancestors of modern crops. Crop plants show a substantial loss of genetic diversity during domestication. CWRs have the ability to tolerate biotic and abiotic stresses [2,7,8] and can be easily introgressed into related cultivated plants [5,7,9], providing important genetic resources for plant breeding. Moreover, their functional substances have industrial applications [3].

The genus *Solanum* of the family Solanaceae contains approximately 1400 species, most of which are distributed in tropical and subtropical regions [10,11].

Twenty-one species of *Solanum* are distributed in Korea, including three natives (e.g., *S. lyratum* Thunb. and *S. japonense* Nakai), nine aliens (e.g., *S. nigrum* L., *S. sarrachoides* Sendtn., *S. americanum* Mill., and *S. viarum* Dunal), and nine cultivated species (e.g., *S. melongena* L., *S. tuberosum* L., and *S. lycopersicum* L.). *Solanum* species are important resources for food and medicinal purposes [12–14]. In particular, *S. tuberosum* (potato) and *S. melongena* (eggplant) are among the most important crops worldwide and have been studied extensively [15–17]. Wild *Solanum* species, as relatives of cultivated plants, contain numerous bioactive compounds, such as steroidal alkaloids and saponins, and have antioxidant properties [11,18,19]. These species possess both agronomic and pharmacological value and are important genetic resources for future breeding and industrial applications. Most studies on species of *Solanum* distributed in Korea have focused on their pharmacological properties [20–22]. Therefore, studies focused on practical mass propagation using in situ conservation and ex situ conservation strategies are critical. However, little is known about the germination characteristics of Korean *Solanum* species under in vitro conditions and dormancy classes, despite implications for the conservation of genetic resources for breeding and industrial applications.

Seed germination is an essential process by which a seed develops into a new plant [23], and it is necessary for the effective conservation of species, the maintenance of genetic diversity, and practical mass propagation [24]. Seed germination is affected by various factors, such as temperature, moisture, humidity, and light, with seed dormancy being the most significant factor [25]. Seed dormancy is a state in which a seed fails to germinate, even under favorable conditions, and it contributes to survival under unfavorable environmental conditions [23,25–28]. Globally, 50–90% of wild species produce dormant seeds depending on their geographic location and exhibit various classes, levels and types of dormancy [29,30]. Seed dormancy is classified based on the developmental status of the embryo, water absorption capacity, and hormonal interactions between internal and external phytohormones in the seeds [23,25,26,31,32]. Baskin and Baskin classified seed dormancy into five classes considering morphological and physiological factors: physical dormancy (PY) caused by the impermeability of covering layers of seeds, morphological dormancy (MD) caused by an immature embryo, physiological dormancy (PD) caused by a physiological inhibitory mechanism in the embryo, morphophysiological dormancy (MPD) resulting from interactions between morphological and physiological dormancy, and combinational dormancy (PY + PD) caused by combined effect of physical and physiological dormancy. In addition, PD, MD and combinational dormancy classes are further divided into levels and then into types: levels include nondeep, intermediate, deep, nondeep epicotyl, deep epicotyl, and deep simple double; types range from Type 1 to Type 6 [26,32,33].

Due to global warming, climate change, and urbanization, forests are being destroyed, threatening the natural habitats of wild species with rich genetic diversity [6,9,24]. As wild plants serve as crucial resources of valuable traits, their conservation is becoming increasingly important [34]. In particular, ex situ conservation, defined as the conservation of biodiversity components outside of their natural habitats, typically via seed banks, requires both basic data on seed germination characteristics and efficient seed propagation methods [35–37]. The genus *Solanum* contains numerous wild species that are genetically related to important cultivated crops, such as tomato, potato, and eggplant [38]. In particular, *S. lyratum* Thunb., *S. japonense* Nakai, *S. nigrum* L., *S. sarrachoides* Sendtn., *S. americanum* Mill., and *S. viarum* Dunal are CWRs found in Korean forests. However, basic research on their seed germination characteristics and dormancy class, important for ex situ conservation, is lacking.

The aim of this study was to investigate germination characteristics and dormancy class in 6 *Solanum* species distributed in Korea. We assessed (1) the external and internal morphological characteristics of seeds, (2) effects of temperature treatments on seed germination characteristics, and (3) effects of cold stratification and gibberellic acid (GA₃) on dormancy release. Our findings provide a reference for the utilization of seed genetic resources, the development of effective mass propagation protocols, and seed-based ex situ conservation.

2. Materials and Methods

2.1. Seed Material

To investigate seed dormancy and germination characteristics, 6 *Solanum* species were evaluated. In particular, *Solanum lyratum* Thunb., *S. japonense* Nakai, *S. nigrum* L., *S. sarrachoides* Sendtn., *S. americanum* Mill., and *S. viarum* Dunal. were obtained from the seed bank (−20 °C, relative humidity 40%) at Baekdudaegan National Arboretum, Bonghwa, Gyeongsangbuk-do, Korea (Table 1). The seeds packed in aluminum envelopes were stored at 4 °C until the start of the experiment in January 2024. Before being deposited in the seed bank, all seeds used in the experiments were carefully cleaned through washing, sieving, and hand selection to ensure quality, and no disinfection process was applied in order to avoid chemical influence and to objectively assess seed dormancy.

Table 1. Seed collection information on the 6 *Solanum* species.

Accession	Scientific Name	Common Name (Korean Name)	Collection Date	Site of Collection
1498	<i>Solanum lyratum</i> Thunb.	Lyre-leaf nightshade (배풍등)	28 October 2022	Uijeongbu-si
1492	<i>Solanum japonense</i> Nakai	Narrow-leaf nightshade (좁은잎배풍등)	24 November 2022	Yangsan-si
1551	<i>Solanum nigrum</i> L.	Poisonberry (까마중)	17 October 2022	Gongju-si
1587	<i>Solanum sarrachoides</i> Sendtn.	Hairy nightshade (털까마중)	14 September 2022	Dongducheon-si
1440	<i>Solanum americanum</i> Mill.	American black (미국까마중)	8 October 2022	Jincheon-gun
1593	<i>Solanum viarum</i> Dunal	Tropical soda apple (왕도깨비가지)	1 December 2022	Jeju-do

2.2. Analysis of Internal and External Seed Morphoanatomy

To evaluate the internal morphology, seeds were cut along their major axes using a stainless-steel razor blade (ST-300, DORCO, Seoul, Republic of Korea) in the initial stage and after germination. The surface and cross-section of the seeds were photographed using a digital microscope (DMV6a, Leica Microsystems, Wetzlar, Germany). The length and width of 100 seeds were determined using a seed scanner (VideometerLab4, VideometerLab, Copenhagen, Denmark). The weight of 1000 seeds was measured using an electronic balance.

2.3. Water Imbibition Test

To evaluate seed permeability under laboratory conditions (approximately 25 ± 2 °C), a water imbibition test was conducted. Four replicates of 25 seeds each were used. The dry matter of the seeds was measured using an electronic balance. Subsequently, the

seeds were placed on two layers of filter paper (Qualitative Filter Papers No. 1, TOYO ROSHI KAISHA, Tokyo, Japan) moistened with distilled water in 90 mm × 15 mm plastic Petri dishes (SPL Life Sciences, Pocheon, Republic of Korea). Water on seed surfaces was removed using paper towels, and the increase in mass due to water absorption was determined by weighing the seeds after 2, 4, 6, 8, 12, and 24 h of incubation. The water absorption rate of seeds was calculated using the following formula:

$$W_s [\%] = [(W_i - W_a)/W_a] \times 100 \quad (1)$$

where W_s is the percent increase in seed mass, W_i is the mass of the seeds after imbibition for a given interval, and W_a is the initial seed mass before water absorption.

2.4. Effect of Incubation Temperature on Seed Germination

To investigate the optimum temperatures for seed germination, a germination test was performed under various temperature conditions (5 °C, 15/6 °C, 20/10 °C or 25/15 °C) for 60 days in multi-room chambers. Temperature and light-controlled multi-room chambers (SJ-404ML, SEJONG SCIENTIFIC, Bucheon, Republic of Korea) set to 5 °C and 12 h/12 h (light/dark) with fluorescent lamps at $50 \pm 3 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ PPFD as well as multi-room chambers (TGC-130H Espec Mic Corp, Osaka, Japan) set to 15/6 °C, 20/10 °C, 25/15 °C and 12 h/12 h (light/dark) with fluorescent lamps at $59.6 \pm 6 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ PPFD. Germination experiments were performed by incubating 4 replicates of 20–25 seeds each in plastic Petri dishes, with some seeds unintentionally lost during the sowing process. These dishes were half-filled with 1% agar (Sigma-Aldrich, St. Louis, MO, USA) and sealed with sealing tape (KS-S3166, Kisanbio, Seoul, Republic of Korea) during the incubation period.

2.5. Effect of Cold Stratification on Seed Germination

To evaluate the impact of cold stratification on dormancy release seeds were stratified for 0, 4, 8, or 12 weeks at 5 °C and 24 h (dark). For each duration of cold stratification, 4 replicates of 25 seeds were placed in plastic Petri dishes (90 × 15 mm) filled with 1% agar medium. The plastic Petri dishes were sealed with sealing tape during incubation. After each cold stratification period, the seeds were transferred to multi-room chambers set to 25/15 °C and 12 h/12 h (light/dark) and incubated for 60 days.

2.6. Effect of GA₃ on Seed Germination

To identify the impact of GA₃ on dormancy release and germination, GA₃ (G4880, Sigma-Aldrich) solutions were prepared at four concentrations (0, 10, 100, or 1000 mg·L^{−1}). The seeds were soaked in each GA₃ solution for 24 h under laboratory conditions (approximately 25 ± 2 °C) and then rinsed with distilled water. Then, 4 replicates of 25 seeds were placed in plastic Petri dishes (90 × 15 mm) filled with 1% agar medium and the Petri dishes were sealed with sealing tape. The seeds were transferred to multi-room chambers set to 25/15 °C and 12 h/12 h (light/dark) and incubated for 60 days.

2.7. Data Collection and Germination Assay

The percentage of germination (radicle protrusion from seeds) was measured every 24 h for 60 days. Each seed was considered to have germinated when the protruding radicle reached a minimum size of 1 mm. To assay germination, biological parameters, such as the germination percentage (GP), mean germination time (MGT), and germination speed (GS), were calculated using the following formulas:

$$\text{GP} (\%) = (N/S) \times 100 \quad (2)$$

$$\text{MGT (days)} = \Sigma (\text{Tx} \cdot \text{Nx}) / \text{N} \quad (3)$$

$$\text{GS} = \Sigma (\text{Nx} / \text{Tx}) \quad (4)$$

where N is the total number of seeds that germinated 60 days after sowing, S is the total number of seeds, Tx is the time in days from day one to the final day of the germination test, and Nx is the total number of germinated seeds on day Tx.

2.8. Statistical Analysis

All data were analyzed using Statistical Package for the Social Sciences (SPSS) version 23 software (IBM Corporation, Armonk, NY, USA). A one-way analysis of variance (ANOVA) was used to test the effect of various factors on the GP, MGR, and GS, followed by Duncan's multiple range tests ($p \leq 0.05$) for post hoc analyses. Graphs were generated using SigmaPlot 10.0 (SPSS Inc., Chicago, IL, USA).

3. Results

3.1. Internal and External Seed Morphoanatomy

The seeds of all 6 *Solanum* species had a reniform shape and an axial-linear-coiled embryo, which was curved or coiled inward. The seed coat was yellow in *S. lyratum*, *S. japonense*, *S. nigrum*, *S. sarrachoides*, and *S. americanum* and brown in *S. viarum*. The morphology and elongation of the embryo remained unchanged from dispersal to the immediate post-germination stage (Figure 1). Seeds of *Solanum* species ranged from 1.44 to 2.48 mm in length (Table 2) and 1.12 to 2.13 mm in width, with a weight of 0.63 to 1.93 g per 1000 seeds.

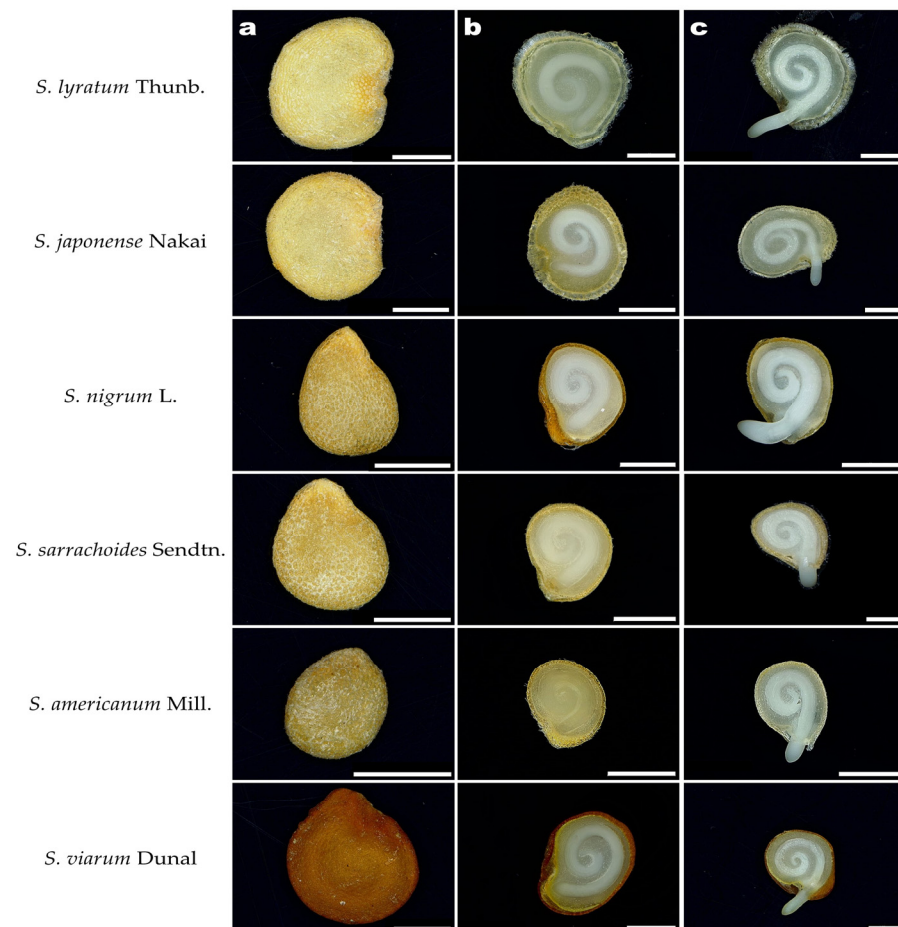


Figure 1. Seed morphology of 6 *Solanum* species. External structure of seeds at dispersal (a), internal structure of seeds at dispersal (b), internal structure after germination (c). Scale bars represent 1 mm.

Table 2. Seed characteristics for 6 *Solanum* species.

Scientific Name	Common Name (Korean Name)	Length (mm)	Width (mm)	1000 Seed Weight (g)
<i>Solanum lyratum</i>	Lyre-leaf nightshade (배풍등)	2.46 ± 0.02^z	2.13 ± 0.02^z	1.68 ± 0.01^y
<i>Solanum japonense</i>	Narrow-leaf nightshade (좁은잎배풍등)	2.37 ± 0.02	2.01 ± 0.02	1.39 ± 0.01
<i>Solanum nigrum</i>	Poisonberry (까마중)	1.83 ± 0.01	1.38 ± 0.01	0.77 ± 0.01
<i>Solanum sarrachoides</i>	Hairy nightshade (털까마중)	1.91 ± 0.01	1.49 ± 0.01	0.69 ± 0.00
<i>Solanum americanum</i>	American black (미국까마중)	1.44 ± 0.01	1.12 ± 0.01	0.63 ± 0.00
<i>Solanum viarum</i>	Tropical soda apple (왕도깨비가지)	2.48 ± 0.01	2.09 ± 0.01	1.93 ± 0.01

^z Values are expressed as the mean $\pm$ standard error ($n = 10$). ^y Values are expressed as the mean $\pm$ standard error ($n = 4$).

3.2. Water Imbibition Test

After 2 h, seeds of all *Solanum* species had absorbed a significant amount of water (Figure 2). The masses of *S. lyratum*, *S. japonense*, *S. nigrum*, *S. sarrachoides*, *S. americanum*, and *S. viarum* seeds increased by 35.0%, 30.7%, 40.8%, 31.0%, 8.4%, and 25.9% after 2 h and by 50.3%, 58.8%, 64.8%, 52.6%, 44.8%, and 44.5% within 24 h, respectively.

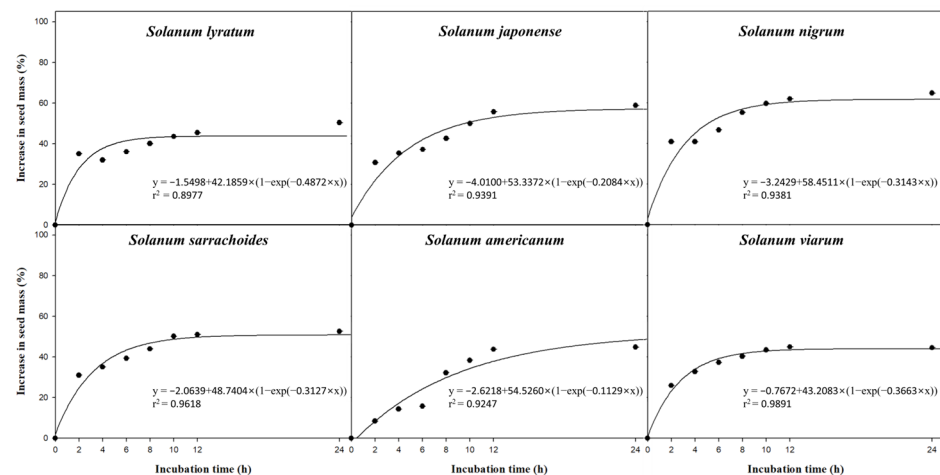


Figure 2. Imbibition curves for seeds of 6 *Solanum* species. The seeds were placed at room temperature (approximately 22–25 °C) on filter paper with distilled water for 24 h. The vertical error bars represent standard errors ($n = 4$).

3.3. Effect of Incubation Temperature on Seed Germination

Germination characteristics under four temperatures (5 °C, 15/6 °C, 20/10 °C, or 25/15 °C) differed among the 6 *Solanum* species (Figure 3, Table 3). Seeds did not germinate at 5 °C within 30 days and showed germination of less than 1% after 60 days in all species except for *S. sarrachoides* (63.3% at 5 °C after 60 days). The seeds of *S. lyratum* germinated only at 15/6 °C after 30 days. The final germination of *S. japonense* seeds was highest at 15/6 °C, reaching 46.0%. *S. nigrum*, *S. americanum*, and *S. viarum* seeds started to germinate within 30 days and showed a greater tendency to germinate at higher temperatures (20/10 °C and 25/15 °C) than at 15/6 °C. The final germination of *S. sarrachoides* seeds

was over 98% at 15/6 °C, 20/10 °C, and 25/15 °C. The MGT and GS values for *S. lyratum* and *S. japonense* were calculated only at 15/6 °C, as germination at other temperatures was insufficient for analyses. Thus, germination in these species was not dependent on temperature and occurred only within a narrow optimal range. By contrast, the MGT of *S. nigrum*, *S. sarrachoides*, *S. americanum*, and *S. viarum* decreased and the GS increased with increasing incubation temperatures. In particular, *S. sarrachoides* showed sufficient germination even at 5 °C. The results indicate that high temperatures promoted dormancy release and increased germination efficiency.

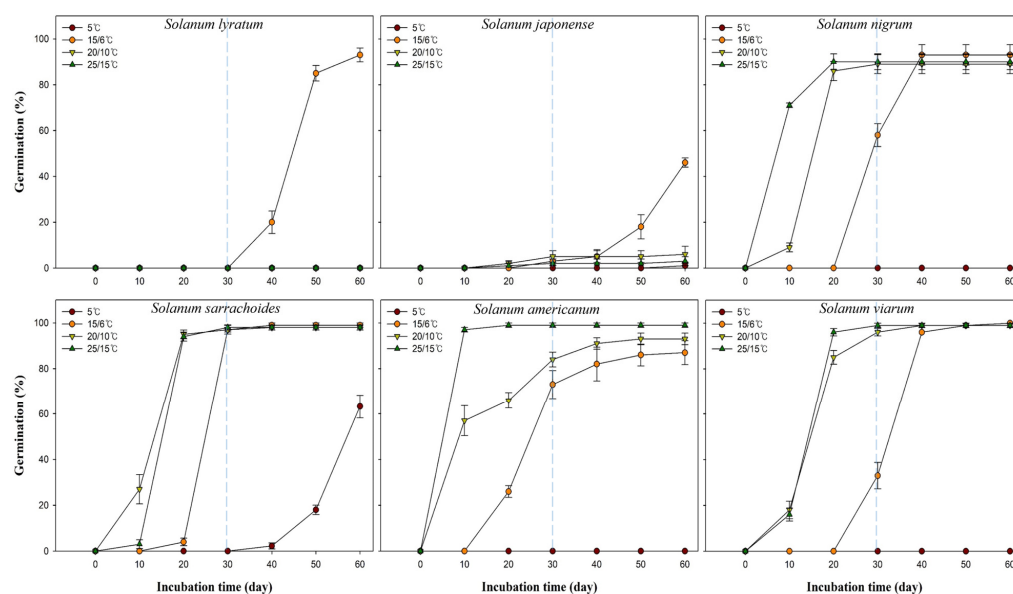


Figure 3. Effect of incubation at 5 °C, 15/6 °C, 20/10 °C, or 25/15 °C on seed germination in 6 *Solanum* species. Error bars indicate means $\pm$ S.E ($n = 4$). Dotted lines indicate 30 days after incubation.

Table 3. Effect of incubation temperature on seed germination parameters in *Solanum* species.

Species	Temperature (°C)	GP ^z at 30 Days (%)	GP at 60 Days (%)	MGT ^y (Days)	GS ^x
<i>Solanum lyratum</i>	5	0.0 $\pm$ 0.00	0.0 $\pm$ 0.00 b	-	-
	15/6	0.0 $\pm$ 0.00	93.0 $\pm$ 3.00 a	44.0 $\pm$ 0.72	0.5 $\pm$ 0.02
	20/10	0.0 $\pm$ 0.00	0.0 $\pm$ 0.00 b	-	-
	25/15	0.0 $\pm$ 0.00	0.0 $\pm$ 0.00 b	-	-
<i>Solanum japonense</i>	5	0.0 $\pm$ 0.00 a ^w	1.0 $\pm$ 1.00 b	-	-
	15/6	3.0 $\pm$ 1.91 a	46.0 $\pm$ 2.00 a	50.9 $\pm$ 1.90	0.2 $\pm$ 0.01
	20/10	5.0 $\pm$ 2.52 a	6.0 $\pm$ 3.46 b	-	-
	25/15	2.0 $\pm$ 2.00 a	3.0 $\pm$ 1.91 b	-	-
<i>Solanum nigrum</i>	5	0.0 $\pm$ 0.00 c	0.0 $\pm$ 0.00 b	-	-
	15/6	58.0 $\pm$ 5.03 b	93.0 $\pm$ 4.43 a	30.3 $\pm$ 0.66 a	0.8 $\pm$ 0.03 c
	20/10	89.0 $\pm$ 4.12 a	89.0 $\pm$ 4.12 a	13.9 $\pm$ 0.08 b	1.7 $\pm$ 0.07 b
	25/15	90.0 $\pm$ 3.46 a	90.0 $\pm$ 3.46 a	9.3 $\pm$ 0.11 c	2.5 $\pm$ 0.10 a
<i>Solanum sarrachoides</i>	5	0.0 $\pm$ 0.00 b	63.3 $\pm$ 5.02 b	52.6 $\pm$ 0.37 a	0.3 $\pm$ 0.02 d
	15/6	97.0 $\pm$ 1.00 a	99.0 $\pm$ 1.00 a	22.3 $\pm$ 0.20 b	1.1 $\pm$ 0.02 c
	20/10	97.0 $\pm$ 1.91 a	98.0 $\pm$ 1.15 a	12.9 $\pm$ 0.50 d	2.0 $\pm$ 0.10 a
	25/15	98.0 $\pm$ 1.15 a	98.0 $\pm$ 1.15 a	15.7 $\pm$ 0.22 c	1.6 $\pm$ 0.05 b
<i>Solanum americanum</i>	5	0.0 $\pm$ 0.00 d	0.0 $\pm$ 0.00 c	-	-
	15/6	73.0 $\pm$ 6.19 c	87.0 $\pm$ 5.26 b	23.7 $\pm$ 0.90 a	1.0 $\pm$ 0.07 c
	20/10	84.0 $\pm$ 3.27 b	93.0 $\pm$ 2.52 ab	14.9 $\pm$ 1.23 b	2.1 $\pm$ 0.11 b
	25/15	99.0 $\pm$ 1.00 a	99.0 $\pm$ 1.00 a	7.1 $\pm$ 0.10 c	3.6 $\pm$ 0.06 a

Table 3. Cont.

Species	Temperature (°C)	GP ^z at 30 Days (%)	GP at 60 Days (%)	MGT ^y (Days)	GS ^x
<i>Solanum viarum</i>	5	0.0 ± 0.00 c	0.0 ± 0.00 b	-	-
	15/6	33.0 ± 5.74 b	100.0 ± 0.00 a	33.5 ± 0.37 a	0.8 ± 0.01 c
	20/10	96.0 ± 1.63 a	99.0 ± 1.00 a	15.3 ± 0.58 b	1.8 ± 0.05 b
	25/15	99.0 ± 1.00 a	99.0 ± 1.00 a	13.6 ± 0.11 c	1.9 ± 0.04 a

^z GP, Germination percentage. ^y MGT, Mean germination time. Values at which germination was extremely low or did not occur were not included in the calculation and are indicated by "-". ^x GS, Germination speed. Values at which germination was extremely low or did not occur were not included in the calculation and are indicated by "-". ^w Means within each column followed by the different letters are significantly different according to Duncan's multiple range test at $p < 0.05$.

3.4. Effect of Cold Stratification on Seed Germination

The germination characteristics under four cold stratification treatments (0, 4, 8, or 12 weeks at 5 °C) differed among the 6 *Solanum* species (Figure 4, Table 4). The seeds of all *Solanum* species germinated within 30 days after cold stratification treatments (≥ 4 weeks). The germination in *S. lyratum* and *S. japonense* increased significantly after at least 4 weeks of cold stratification. The final germination for *S. lyratum* and *S. japonense* without cold stratification (0 weeks) were 0% and 3%, respectively, while those for seeds incubated at 25/15 °C after cold stratification ranged from 91% to 99% for *S. lyratum* and 26% to 62% for *S. japonense* within 30 days. The final germination for *S. nigrum*, *S. americanum*, *S. sarrachoides*, and *S. viarum* seeds incubated at 25/15 °C after cold stratification ranged from 87% to 100%, regardless of the cold stratification period. Without cold stratification, the MGT and GS values for *S. lyratum* and *S. japonense* could not be calculated owing to insufficient germination. However, after cold stratification for more than 4 weeks, these values became measurable. In particular, seeds with 12 weeks of cold stratification exhibited the shortest MGT and highest GS, indicating that cold stratification promoted dormancy release and improved germination efficiency. By contrast, cold stratification did not influence germination in *S. nigrum*, *S. sarrachoides*, *S. americanum*, or *S. viarum*. However, seeds with 12 weeks of stratification exhibited the shortest MGT values, indicating that cold stratification increased germination efficiency even if it did not play a major role in dormancy release.

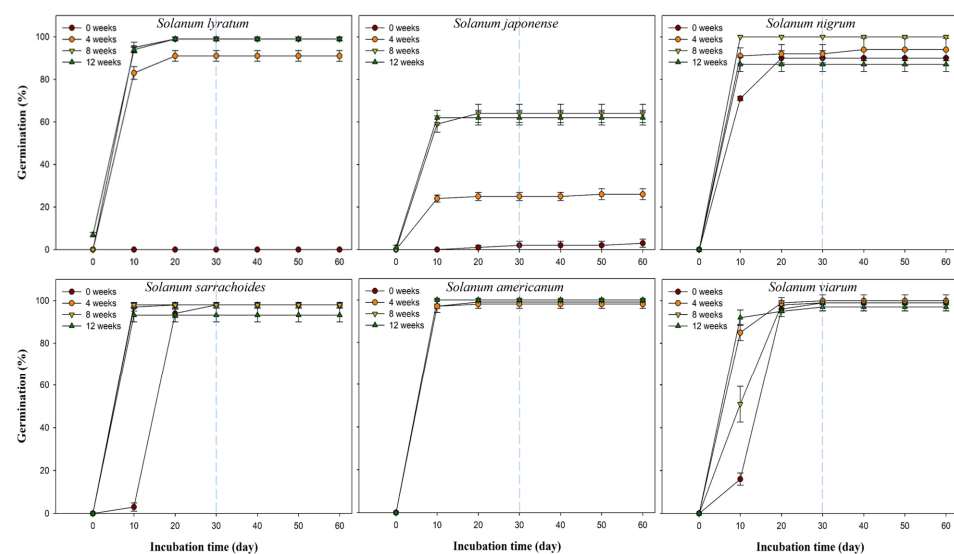


Figure 4. Effect of cold stratification (0, 4, 8, or 12 weeks at 5 °C) on seed germination in 6 *Solanum* species. Seeds were incubated for 60 days at 25/15 °C (light/dark, 12 h/12 h). Error bars indicate mean ± S.E ($n = 4$). Dotted lines indicate 30 days after incubation.

Table 4. Effect of cold stratification on seed germination parameters of *Solanum* species.

Species	Duration of Cold Stratification (Weeks) at 5 °C	GP ^z at 30 Days (%)	GP at 60 Days (%)	MGT ^y (Days)	GS ^x
<i>Solanum lyratum</i>	0	0.0 ± 0.00 c	0.0 ± 0.00 c	-	-
	4	91.0 ± 2.52 b	91.0 ± 2.52 b	8.1 ± 0.14 a	3.0 ± 0.12 b
	8	99.0 ± 1.00 a ^w	99.0 ± 1.00 a	7.3 ± 0.07 b	3.6 ± 0.05 b
	12	99.0 ± 1.00 a	99.0 ± 1.00 a	3.4 ± 0.05 c	11.7 ± 0.44 a
<i>Solanum japonense</i>	0	2.0 ± 2.00 c	3.0 ± 1.91 c	-	-
	4	25.0 ± 1.91 b	26.0 ± 2.58 b	8.5 ± 1.77 a	0.9 ± 0.11 c
	8	64.0 ± 4.32 a	64.0 ± 4.32 a	6.4 ± 0.08 a	2.8 ± 0.19 b
	12	62.0 ± 3.46 a	62.0 ± 3.46 a	4.3 ± 0.18 a	5.0 ± 0.51 a
<i>Solanum nigrum</i>	0	90.0 ± 3.46 ab	90.0 ± 3.46 ab	9.3 ± 0.11 a	2.5 ± 0.10 c
	4	92.0 ± 4.32 ab	94.0 ± 5.29 ab	5.0 ± 0.59 b	5.8 ± 0.22 b
	8	100.0 ± 0.00 a	100.0 ± 0.00 a	3.4 ± 0.07 c	7.7 ± 0.18 a
	12	87.0 ± 3.42 b	87.0 ± 3.42 b	4.0 ± 0.23 c	6.2 ± 0.27 b
<i>Solanum sarrachoides</i>	0	98.0 ± 1.15 a	98.0 ± 1.15 a	15.7 ± 0.22 a	1.6 ± 0.05 c
	4	98.0 ± 1.15 a	98.0 ± 1.15 a	3.0 ± 0.07 b	9.0 ± 0.17 b
	8	98.0 ± 1.15 a	98.0 ± 1.15 a	2.8 ± 0.04 b	9.0 ± 0.21 b
	12	93.3 ± 3.20 a	93.3 ± 3.20 a	1.1 ± 0.05 c	21.1 ± 1.82 a
<i>Solanum americanum</i>	0	99.0 ± 1.00 a	99.0 ± 1.00 a	7.1 ± 0.10 a	3.6 ± 0.06 c
	4	98.0 ± 2.00 a	98.0 ± 2.00 a	3.2 ± 0.07 c	7.8 ± 0.19 b
	8	100.0 ± 0.00 a	100.0 ± 0.00 a	3.6 ± 0.04 b	7.2 ± 0.03 b
	12	100.0 ± 0.00 a	100.0 ± 0.00 a	2.8 ± 0.06 d	9.5 ± 0.32 a
<i>Solanum viarum</i>	0	99.0 ± 1.00 a	99.0 ± 1.00 a	13.6 ± 0.11 a	1.9 ± 0.04 d
	4	100.0 ± 0.00 a	100.0 ± 0.00 a	9.0 ± 0.22 c	2.9 ± 0.06 b
	8	99.0 ± 3.79 a	99.0 ± 3.79 a	11.3 ± 0.21 b	2.3 ± 0.13 c
	12	97.0 ± 1.91 a	97.0 ± 1.91 a	7.2 ± 0.28 d	3.7 ± 0.13 a

^z GP, Germination percentage. ^y MGT, Mean germination time. Values at which germination was extremely low or did not occur were not included in the calculation and are indicated by "-". ^x GS, Germination speed. Values at which germination was extremely low or did not occur were not included in the calculation and are indicated by "-". ^w Means within each column followed by the different letters are significantly different according to Duncan's multiple range test at $p < 0.05$.

3.5. Effect of GA₃ on Seed Germination

The germination characteristics under four GA₃ concentrations (0, 10, 100, or 1000 mg·L⁻¹) differed among the 6 *Solanum* species (Figure 5, Table 5). Seeds of *S. lyratum* and *S. japonense* showed significantly higher germination than those in the control (0 mg·L⁻¹) only at the highest GA₃ concentration (1000 mg·L⁻¹). The final germination of *S. lyratum* and *S. japonense* seeds treated with 1000 mg·L⁻¹ GA₃ reached 99% and 79%, respectively, while that of seeds treated with lower concentrations (0, 10, and 100 mg·L⁻¹) showed germination of less than 5% for *S. lyratum* and 12% for *S. japonense*. The final germination of *S. nigrum*, *S. americanum*, *S. sarrachoides*, and *S. viarum* seeds ranged from 77% to 100%, regardless of GA₃ concentrations. The MGT and GS values for *S. lyratum* and *S. japonense* were calculated only at 1000 mg·L⁻¹, as germination at other concentrations was insufficient for analyses. These results suggest that high concentration of GA₃ not only promoted dormancy release but also improved germination efficiency. By contrast, the GA₃ concentration did not affect germination in *S. nigrum*, *S. sarrachoides*, *S. americanum*, or *S. viarum*. However, seeds treated with 1000 mg·L⁻¹ GA₃ exhibited the shortest MGT values and highest GS, indicating that GA₃ treatment increased germination efficiency even if it did not play a major role in dormancy release.

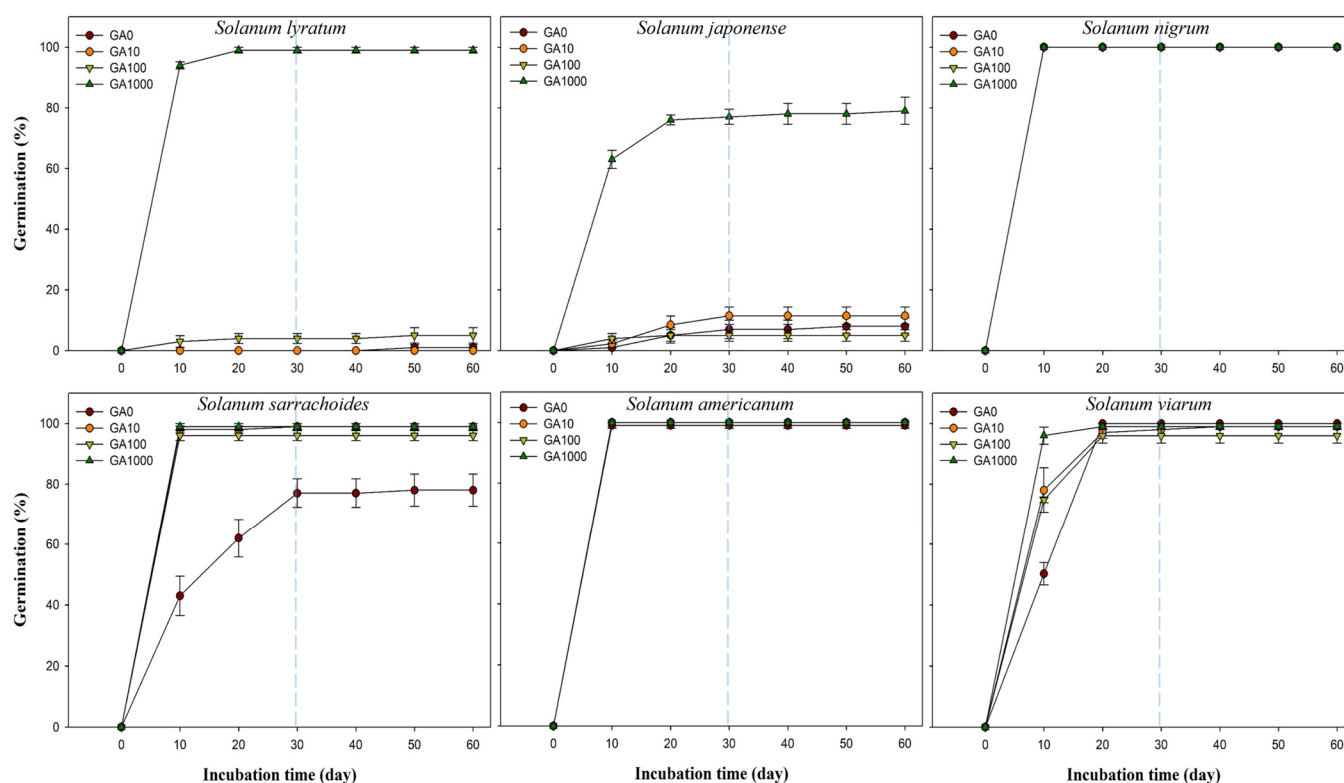


Figure 5. Effect of GA₃ (0, 10, 100, or 1000 mg·L^{−1}) on seed germination in 6 *Solanum* species. Seeds were soaked in a GA₃ solution for 24 h and then incubated for 60 days at 25/15 °C. Error bars indicate means ± S.E. (*n* = 4). Dotted lines indicate 30 days after incubation.

Table 5. Effect of GA₃ on seed germination parameters in *Solanum* species. Seeds were soaked in a GA₃ (0, 10, 100, or 1000 mg·L^{−1}) solution for 24 h at room temperature and then incubated for 60 days at 25/15 °C (light/dark, 12 h/12 h).

Species	GA ₃ Concentration (mg·L ^{−1})	GP ^z at 30 Days (%)	GP at 60 Days (%)	MGT ^y (Days)	GS ^x
<i>Solanum lyratum</i>	0	0.0 ± 0.00 c	1.0 ± 1.00 bc	-	-
	10	0.0 ± 0.00 c	0.0 ± 0.00 c	-	-
	100	4.0 ± 1.63 b	5.0 ± 2.52 b	-	-
	1000	99.0 ± 1.00 a ^w	99.0 ± 1.00 a	7.3 ± 0.23	3.5 ± 0.09
<i>Solanum japonense</i>	0	7.0 ± 3.00 b	8.0 ± 2.83 b	-	-
	10	11.5 ± 2.87 b	11.5 ± 2.87 b	-	-
	100	5.0 ± 1.91 b	5.0 ± 1.91 b	-	-
	1000	77.0 ± 2.52 a	79.0 ± 4.43 a	8.7 ± 0.94	2.7 ± 0.09
<i>Solanum nigrum</i>	0	100.0 ± 0.00	100.0 ± 0.00	6.9 ± 0.16 b	3.7 ± 0.09 b
	10	100.0 ± 0.00	100.0 ± 0.00	7.5 ± 0.10 a	3.4 ± 0.03 b
	100	100.0 ± 0.00	100.0 ± 0.00	7.0 ± 0.07 b	3.5 ± 0.22 b
	1000	100.0 ± 0.00	100.0 ± 0.00	5.3 ± 0.06 c	4.9 ± 0.09 a
<i>Solanum sarrachoides</i>	0	77.0 ± 4.73 b	78.0 ± 5.29 b	14.9 ± 0.74 a	1.7 ± 0.15 c
	10	99.0 ± 1.00 a	99.0 ± 1.00 a	7.4 ± 0.07 b	3.5 ± 0.10 b
	100	96.0 ± 1.63 a	96.0 ± 1.63 a	7.0 ± 0.08 b	3.7 ± 0.10 b
	1000	99.0 ± 1.04 a	99.0 ± 1.04 a	3.9 ± 0.03 c	6.3 ± 0.12 a
<i>Solanum americanum</i>	0	99.0 ± 1.00 a	99.0 ± 1.00 a	5.2 ± 0.07 b	4.8 ± 0.05 b
	10	100.0 ± 0.00 a	100.0 ± 0.00 a	5.6 ± 0.09 a	4.6 ± 0.06 c
	100	100.0 ± 0.00 a	100.0 ± 0.00 a	5.1 ± 0.07 b	5.0 ± 0.07 b
	1000	100.0 ± 0.00 a	100.0 ± 0.00 a	3.9 ± 0.02 c	6.5 ± 0.04 a

Table 5. Cont.

Species	GA ₃ Concentration (mg·L ⁻¹)	GP ^z at 30 Days (%)	GP at 60 Days (%)	MGT ^y (Days)	GS ^x
<i>Solanum viarum</i>	0	100.0 ± 0.00 a	100.0 ± 0.00 a	10.7 ± 0.38 a	2.4 ± 0.20 c
	10	98.0 ± 2.00 a	99.0 ± 1.00 a	9.8 ± 0.59 ab	2.7 ± 0.13 bc
	100	95.9 ± 2.36 a	95.9 ± 2.36 a	8.8 ± 0.21 b	2.9 ± 0.09 b
	1000	99.0 ± 1.00 a	99.0 ± 1.00 a	6.1 ± 0.21 c	4.5 ± 0.15 a

^z GP, Germination percentage. ^y MGT, Mean germination time. Values at which germination was extremely low or did not occur were not included in the calculation and are indicated by “-”. ^x GS, Germination speed. Values at which germination was extremely low or did not occur were not included in the calculation and are indicated by “-”. ^w Means within each column followed by the different letters are significantly different according to Duncan’s multiple range test at $p < 0.05$.

4. Discussion

The seed morphology of *Solanum* species in Korea matched that in previous reports, with a reniform or obovoid shape and yellow or brown color [10,39]. According to Martin, *S. verbascifolium*, *S. nigrum*, and *S. dulcamara* possess curved linear-type embryos [40]. The embryos of *S. japonense* and *S. lyratum* have been described as axial-linear-coiled [39]. The 6 *Solanum* species evaluated in this study exhibited axial-linear-coiled embryos, characterized by more than one full turn of coiling.

Seed dormancy refers to the inability to germinate in a specified period of time under environmental conditions (temperature, water, etc.) that otherwise are favorable for germination [23,25,41]. Baskin and Baskin classified seed dormancy into five types: MD, PY, PD, MPD, and PY + PD [26,33,42–44]. Since the seeds of the six species had a fully developed embryo, they do not have MD or MPD. Also, since seeds imbibed water, they do not have PY or PY + PD.

PD is reported to be caused by a physiological inhibitory mechanism in the embryo. Seeds with PD are water-permeable, have a mature embryo, and require more than 30 days for germination [33,45]. *Solanum* species with PD and non-deep PD have been reported [20,46,47]. In this study, the germination of *S. lyratum* and *S. japonense* seeds was delayed for more than 30 days under all temperature treatments. Relatively large portions of *S. nigrum*, *S. americanum*, and *S. viarum* seeds germinated within 30 days, and the germination percentage and speed increased as the temperature increased from 15/6 °C to 25/15 °C. The seeds of *S. sarrachoides* germinated to over 90% under all temperature conditions except 5 °C within 30 days. These results indicate that the seeds of *S. sarrachoides* are non-dormant, and the seeds of the other five species have PD (Table 6).

Table 6. Summary of seed dormancy and germination traits in 6 *Solanum* taxa based on Baskin & Baskin’s criteria [33] for non-deep PD.

Seed Traits	<i>S. lyratum</i>	<i>S. japonense</i>	<i>S. nigrum</i>	<i>S. sarrachoides</i>	<i>S. americanum</i>	<i>S. viarum</i>
Embryo development	Embryos were axial-linear-coiled and fully developed					
Water absorption	≥30% absorbed water within 24 h					
Germination in 30 days (15/6 °C to 25/15 °C)	0%	2–5%	58–90%	97–98%	73–99%	30–99%
Effect of cold stratification on germination at 25/15 °C	4 °C, ≥4 weeks → ≥90% germination	4 °C, ≥8 weeks → ≥60% germination	≥80% germination (negatively correlated with MGT, positively correlated with GS)			
Effect of GA ₃ treatment on germination at 25/15 °C	GA ₃ 1000 mg·L ⁻¹ → ≥90% germination	GA ₃ 1000 mg·L ⁻¹ → ≥70% germination	≥70% germination (negatively correlated with MGT, positively correlated with GS)			
Dormancy type	Type 1 non-deep PD		Non-deep PD with CD	Non-dormant	Non-deep PD with CD	

PD can be broken through cold or warm stratification, after ripening, or by phytohormone treatment, such as GA₃, GA₄₊₇, or fluridone [23,25,26,29,31,32,43,48]. Seeds dispersed in autumn can usually break dormancy through cold stratification during winter [26]. Gibberellic acids not only counteract the effect of ABA but also stimulate the synthesis of enzymes responsible for cell wall hydrolysis after seed maturation [23]. This process can break down the endosperm barriers and break seed dormancy by promoting radicle emergence. PD can be classified into three levels: deep, intermediate, and non-deep. Deep PD can be broken after a period of 12–24 weeks of cold stratification and cannot be broken by GA₃ treatment. Intermediate PD can be broken after period of moist-cold stratification (12–16 weeks) and is often responsive GA₃. In some species, germination of seeds with intermediate PD can be further promoted by a period of high-temperature (warm) stratification before cold stratification [33,45]. Non-deep PD can be broken by a relatively short period of warm and/or cold stratification. Depending on the species, non-deep PD can be broken by cold stratification, warm stratification and dry after ripening or GA₃ treatment [26,33,45]. In this study, a cold stratification period of 8 weeks or longer was effective in breaking dormancy and promoting germination in seeds of *S. lyratum* and *S. japonense*. It remains unclear whether this approach promotes the germination of *S. nigrum*, *S. sarrachoides*, *S. americanum*, or *S. viarum* seeds at 15 °C, as the cold-stratified seeds in this study were incubated only at 25/15 °C. However, a cold stratification period of 12 weeks increased the germination efficiency of these species. In the GA₃ experiment, GA₃ 1000 mg·L⁻¹ effectively broke dormancy in *S. lyratum* and *S. japonense* by promoting radicle emergence, and increased the germination efficiency in *S. nigrum*, *S. sarrachoides*, *S. americanum*, and *S. viarum*. Based on these results, the seeds of *S. lyratum* and *S. japonense* were classified as having non-deep PD, which can be broken by short periods of cold stratification and GA₃ treatment. By contrast, at 15/6 °C within 30 days, a portion of the seeds of *S. nigrum*, *S. americanum*, and *S. viarum* germinated. The results indicate that a fraction of the seed population is nondormant, whereas the ungerminated fraction exhibits PD.

Non-deep PD can be classified into 6 types (Type 1–6) based on temperature requirements for germination during the dormancy-breaking process. Seeds of Type 1 germinate only at low temperatures initially, with the maximum germination temperature increasing as the dormancy break progresses. Seeds of Type 2 germinate only at high temperatures initially, with the minimum germination temperature decreasing as the dormancy break progresses [29,45]. In this study, seeds of *S. lyratum* and *S. japonense* germinated at relatively low temperatures (15/6 °C), and germination was delayed at higher temperatures (20/10 °C and 25/15 °C). However, after dormancy was broken by CS or GA₃ treatment, germination occurred at 25/15 °C. These findings suggest that these species exhibit Type 1 non-deep PD.

Conditional dormancy (CD) is an intermediate state between dormancy and non-dormancy. Seeds with CD can germinate within a narrow range of environmental conditions. Once CD is broken, the seeds can germinate over the full range of conditions experienced by the species [29]. The base temperature for germination within 30 days for *S. nigrum*, *S. americanum*, and *S. viarum* is 15/6 °C, and seeds did not germinate below this temperature. Their optimum temperature was 25/15 °C, at which the maximum germination rate was observed. Our results generally matched the previously reported germination characteristics of *S. nigrum* and *S. sarrachoides* [49,50]. These results suggest that the three species have non-deep PD with CD. According to Roberts and Lockett [49] and Roberts and Boddrell [50], seeds of these species exhibit physiological dormancy cycling. However, further research is needed to clarify this topic.

Spicer and Dionne [46] reported that the seeds of *Solanum* species germinated more effectively after GA₃ 1000 mg·L⁻¹ treatment than after GA₃ 100 mg·L⁻¹ treatment using

filter paper, not agar. Lee et al. [20] reported that seed germination in *S. lyratum* decreased as the GA₃ treatment concentration increased when sown in soil. However, our results showed that the seed germination in *S. lyratum* and *S. japonense* is highest after GA₃ 1000 mg·L⁻¹ treatment when agar is used. These results indicate that germination parameters differ depending on the incubation method. In this study, the germination rate of *Solanum* seeds treated with GA₃ 1000 mg·L⁻¹ was similar to that of seeds subjected to 12 weeks of cold stratification, suggesting that GA₃ treatment can be a substitute for prolonged cold stratification. These findings provide useful insights for developing efficient seed germination protocols for the conservation and propagation of *Solanum* species.

5. Conclusions

Overall, the seeds of *S. lyratum* and *S. japonense* exhibited non-deep PD, and their germination increased significantly under cold stratification or treatment with GA₃ 1000 mg·L⁻¹. Additionally, the seeds of *S. nigrum*, *S. americanum*, and *S. viarum* exhibited non-deep PD with CD, and their germination efficiency was higher using cold stratification or GA₃ 1000 mg·L⁻¹ than under temperature treatment alone (at 25/15 °C) in terms of MGT and GS. By contrast, the seeds of *S. sarrachoides* were classified as non-dormant as they germinated under a wide range of temperature conditions. These findings provide a valuable basis for overcoming seed dormancy and establishing effective propagation strategies. Moreover, the insights gained from this study could contribute to the conservation and utilization of wild *Solanum* genetic resources.

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Abbreviations

The following abbreviations are used in this manuscript:

CD	conditional dormancy
CWR	crop wild relatives
GA ₃	gibberellic acid
GP	germination percentage
GS	germination speed
MD	morphological dormancy
MGT	mean germination time
MPD	morphophysiological dormancy
PD	physiological dormancy
PY	physical dormancy

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