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Seed Dormancy and Germination Requirements of *Torilis scabra* (Apiaceae)

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Abstract: The timing of seed germination significantly affects the fitness and life cycle of plants. *Torilis scabra* is a perennial medicinal herb occurring in mixed forests but the increasing use and modification of forestlands in recent decades has led to the degeneration of its natural habitat. Nonetheless, the requirements for germination in *T. scabra* remain unclear. The present study focused on identifying conditions necessary to break *T. scabra* seed dormancy and describing its seed dormancy type. By periodically collecting seeds that were sown in the field, germination phenology was studied. The impact of light, temperature, and warm/cold stratification on breaking seed dormancy and promoting germination was also determined through incubating seeds in laboratory conditions. Additionally, the effect of GA_3 was explored to more accurately identify the type of dormancy present. The results demonstrated that the seeds of *T. scabra* possessed small, undeveloped embryos with physiological dormancy at the time of maturity. In the field, embryo growth initiated in early spring and the embryo–seed length ratio increased by ~300% before the radical emerged. In the laboratory, the embryo–seed length ratio increased from 0.24 to 0.82 when seeds were subjected to cold stratification at 4 °C and then transferred to 15/25 °C. Germination was observed across a broad temperature range after cold stratification. GA_3 also helped to break dormancy but after-ripening did not. Taken together, the results suggest that seeds of *T. scabra* have non-deep simple morphophysiological dormancy.

Keywords: Apiaceae seeds; morphophysiological dormancy; cold stratification; germination phenology; underdeveloped embryo

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1. Introduction

The timing of seed germination significantly affects the fitness and life cycles of plants [1], niche construction [2,3], species coexistence [4,5], and community composition in the presence of climate change [6,7]. Seed dormancy is assumed to be a bet-hedging mechanism in plants allowing them to prevent sibling competition [8,9]. Seeds that are buried within a seed bank can sense several environmental conditions (such as light and temperature), which also adjusts the internal dormancy depth on a continuous basis to synchronize germination and seedling emergence at the appropriate time and space [10–12]. Five categories of dormancy have been identified in line with the classification strategy of seed dormancy: physical (PY), physiological (PD), combinational (PY + PD), morphological (MD), and morphophysiological (MD + PD; MPD) dormancy [13]. Seeds with PD need specific biochemical adjustments in order to overcome a barrier that prevents the embryo from penetrating the fruit or seed coat and germination. PY seeds have an impervious fruit/seed covering, whereas MD seeds have underdeveloped embryos [13].

Apiaceae is a large family, and many seeds within this family have linear and underdeveloped embryos when they are dispersed. These embryos must reach a substantial length before the radicle can emerge, as noted by Martin [14] and Baskin and Baskin [15]. As a result, seeds of this plant family may exhibit either MD or MPD. Furthermore, previous

studies have indicated that even closely related species within this family may display different dormancy types [15–32]. For example, in the subfamily Apioideae, seeds of *Angelica glauca* [16] and *Torilis nodosa* [17] have MD. By contrast, seeds of *Chaerophyllum procumbens* [18], *Selinum carvifolia* [19], *Spermolepis echinata* [15], *Torilis japonica* [20], and *Trepocarpus aethusae* [21] show non-deep simple MPD. Seeds of *Bupleurum aureum* [22] and *Cenolophium denudatum* [23] display deep simple MPD. Seeds of *Osmorhiza claytonii* [24] and *O. longistylis* [25] have non-deep complex MPD. Seeds of *Aegopodium podagraria* [28,29], *Anthriscus sylvestris* [30], *Chaerophyllum aureum* [22], *C. temulum* [19], *Cryptotaenia canadensis* [31], and *Heracleum asperum* [22] have deep complex MPD. Given the variety of dormancy types observed in Apiaceae, laboratory and in-depth field research is required regarding species with unknown dormancy-breaking and germination requirements. This is particularly true for species requiring broadcast seeding with high seed waste [33–35].

Understanding MPD seed germination requires identifying which environmental conditions break dormancy and stimulate embryo development [36]. Dormancy breaking and embryo growth in different plant species may require different combinations of temperature treatments. For example, some species may require cold stratification followed by warm stratification, some may require warm stratification followed by cold stratification, and some may require just one of these treatments [36–40]. Additionally, MPD is divided into nine levels according to the response to gibberellic acid (GA_3), cold/warm stratification requirements, temperature requirements for embryo growth, and time of root and/or shoot emergence [13,15].

Torilis scabra (Apiaceae) is a perennial herb that grows in mixed forests on mountain slopes, in valleys, and on roadsides at elevations of 200–2400 m in China, Japan, and Korea [41]. The young leaves and fruits can be used as a flavoring and produce a sharper flavor than garden chervil. In addition, this species possesses valuable medicinal properties; its roots are traditionally used to treat various ailments such as abdominal pain caused by parasitic worms and rheumatism [42]. However, the increasing market demand for *T. scabra* and unparalleled human damage to the natural environment have threatened the species in recent decades [43]. Furthermore, the seeds of *T. scabra* are dormant and thus have a low germination percentage, resulting in high propagation costs and substantial amounts of seed waste in horticulture. Nevertheless, little is known about the type of dormancy exhibited by this species. Therefore, understanding seed dormancy and germination phenology in *T. scabra* is crucial for species conservation and artificial propagation.

This study focused on investigating essential conditions needed to break dormancy and on determining seed dormancy types exhibited in *T. scabra*. Specifically, we studied (1) the effect of temperature on embryo development, (2) the effects of cold and warm stratification on dormancy breaking and seed germination, (3) the role of dry storage (after-ripening) and gibberellin in dormancy breaking, and (4) germination phenology in the field.

2. Materials and Methods

2.1. Study Area and Seed Collection

Fresh matured seeds of *T. scabra* seeds, also known as "mericarps", were collected from approximately 1000 plants growing in Xinbin County, China (41°56′ N, 125°4′ E) between 1 and 10 September 2018. All the following tests began within two weeks after the seed harvest. The seed moisture content used for experiments was 7.8659 ± 0.2162%. The location of the collection experiences a temperate continental monsoon climate, and the average temperature per year is 7.6 °C. The coldest and warmest months are January and July, with minimum and maximum temperatures of −12.3 °C and 29.7 °C, respectively. The average temperature from May to September, which is the period of plant growth, was 20.7 °C. This area experiences a frost-free period of 130 to 180 days, with an average annual precipitation of 400 to 1000 mm [43].

2.2. Seed Morphology and Mass

Vernier calipers were used to determine the width, length, and thickness of *T. scabra* seeds (n = 20). To measure seed mass, the weight of ten randomly selected samples from 100 seeds was measured using an electronic scale (Sartorius AG, Göttingen, Germany) accurate to within 0.0001 g.

2.3. Imbibition Tests

Water absorption was evaluated in the laboratory for determining whether the fruit/seed coat of *T. scabra* is capable of absorbing water. Four replicates of 25 seeds were weighed using the Sartorius electronic scale before being placed on distilled water-moistened Whatman No. 1 filter papers in plastic Petri dishes (10 cm in diameter). Seeds were removed from the Petri dishes at 0, 0.5, 1, 2, 4, 6, and 8 h, then blotted dry, weighed, and replaced in each dish. The percentage increases in fresh mass (% Wr) were calculated by using the following formula: % Wr = [(Wf − Wi)/Wi] × 100, where Wi represents the initial weight of the seed and Wf refers to the weight of the seed after being dried for a specified period [11].

2.4. General Procedures of the Germination Test

Seeds were incubated under 5/15, 10/20, 15/25, and 20/30 °C conditions in the presence of light (12 h photoperiod/day; hereafter referred to as "light") or continuous darkness to investigate seed germination. For each treatment, four replicates for 25 seeds were placed in the Petri dishes (10 cm in diameter) on two layers of distilled water-saturated Whatman No. 1 filter paper. To reduce water loss, a plastic film was used to wrap dishes. These four temperatures were chosen as they could represent the monthly minimum and maximum air temperatures in the environment of *T. scabra* at the seed collection site and in eastern China [11]. The minimum and maximum temperatures respectively coincided with the diurnal 12-h dark/12-h light photocycle for seeds, which were subjected to incubation under ca. 100 μmol/m^2/s photon irradiance (400–700 nm) of light offered by cool, white-fluorescent tubes. The radicle tip emergence criteria of 1 mm was used to determine germination [15]. Ungerminated seeds were squeezed with forceps at the end of each trial to estimate if they contained one mushy and gray embryo (non-viable) or one solid and white embryo (viable) [38]. Germination percentage was calculated as the number of germinated seeds/(25 − non-viable seeds) × 100%.

2.5. Germination and Embryo Length in Fresh Seeds

T. scabra fresh seeds were cultivated under light and dark conditions under 5/15, 10/20, 15/25, and 20/30 °C for 30 days to determine whether they had MPD or MD. In addition, four replicates of ten seeds were subjected to 24 h incubation onto filter paper under 20–25 °C and RH 40–50% conditions, following which embryo and seed lengths were determined.

2.6. Effects of Temperature on Embryo Growth

To determine how cold/warm temperatures affected embryo growth, 5 mL distilled water was added into a total of 14 Petri dishes each containing 10 seeds, followed by incubation with light under 4 or 15/25 °C at 8 weeks. Thereafter, seeds incubated at 4 °C were transferred to 15/25 °C and seeds incubated at 15/25 °C were placed under 4 °C for an additional 6 weeks. At 2 week intervals, one Petri dish from each temperature setting was selected at random for determining embryo–seed length ratio (E/S) in those 10 seeds.

2.7. Effects of Cold or Warm Stratification on Seed Germination

T. scabra fresh seeds were put in metal boxes (depth, 10 cm; diameter, 20 cm) on rinsed quartz sand between two layers of filter paper and incubated at 4 or 15/25 °C to determine how cold/warm stratification affected germination. Following stratification for 0/2/4/8/12/16 weeks, four replicates of 25 ungerminated seeds were randomly selected from each box and transferred to Petri dishes for a 30 day incubation period in the light and

dark at 5/15, 10/20, 15/25, or 20/30 °C. Germinated seeds were determined and discarded from the Petri dishes.

2.8. Effects of Warm plus Cold Stratification on Seed Germination

Fresh seeds of *T. scabra* were stratified for 0 or 4 weeks under 15/25 °C, followed by transfer to 4 °C for 12 week cold stratification for culture under light and dark conditions at 5/15, 10/20, 15/25, and 20/30 °C for 30 days.

2.9. Effect of Dry Storage (After-Ripening) on Seed Germination

T. scabra fresh seeds were put in lidless Petri dishes at room temperature (20–25 °C, 40–50% RH) for 2, 4, and 8 weeks, followed by 30 day incubation in light under 5/15, 10/20, and 15/25 °C following each after-ripening phase. At the end of the trial, seed germination was analyzed according to the previous description.

2.10. Effects of Gibberellin on Seed Germination

Four replicates of 25 seeds of *T. scabra* were cultivated in Petri dishes for 12 weeks at 15/25 °C in the presence of light. The samples were moistened with a 5 mL 0, 10, 100, or 1000 mgL^{-1} solution of GA_3. Distilled water was used to moisten the filter paper, and germinated seeds were counted and discarded weekly.

2.11. Germination Phenology and Embryo Growth

A total of 60 nylon bags with mesh sizes of 1 mm were filled with fifty seeds each. Each nylon bag was filled in a 1:1 ratio with seeds and sand. During October 2018, bags were buried in field soil at a depth of 2 cm in the experimental garden of Yangzhou University. Each bag's position was noted, and they were distributed among two 1 m^2 plots. Every two weeks, four bags were excavated for counting seeds that had germinated. Under a microscope, ten seeds of each bag were adopted for measuring embryo and seed lengths. After removing any seeds with radicle protrusions from the embryo for measurement, we determined the E/S ratio. A digital thermometer was used to measure the daily air temperatures.

2.12. Statistical Analyses

All analyses were conducted in R version 4.2.2 using the car and multcomp packages. For ensuring the homogeneity of variance, percentages were arcsine transformed before statistical analysis. *t*-test or one-way ANOVA was employed when there were either two treatments ($p < 0.05$) or multiple treatments analyzed by one factor, respectively; two- or three-way ANOVAs were used if there were two or more factors ($p < 0.05$). Upon significant differences detected by ANOVA, we utilized Tukey's HSD test for determining treatment differences ($p < 0.05$).

3. Results

3.1. Seed Morphology and Mass

Seeds of *T. scabra* were elliptical to oblong in shape at maturity; their length was 4.78 ± 0.12 mm, their width was 1.75 ± 0.09 mm, and their thickness was 1.26 ± 0.08 mm. The mass of 1000 seeds was 1.239 ± 0.14 g.

3.2. Imbibition Tests

The seeds absorbed water easily and displayed a typical pattern of initially absorbing water rapidly. Seed mass increased by 45% after 0.5 h and by 82% after 1 h. Water imbibition peaked at 2 h, and seed mass did not increase as more time passed (Figure 1).

3.3. Germination and Embryo Length of Fresh Seeds

Seed germination was not detected at 30 days of incubation under 5/15, 10/20, 15/25, and 20/30 °C, under both light and dark conditions. In comparison with seed length, embryos remained relatively short. The embryos were 1.09 ± 0.14 mm in length and had an E/S ratio of 0.23 ± 0.01.

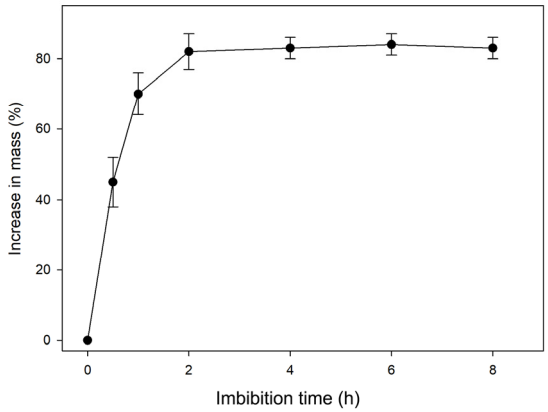

Figure 1. Imbibition curves for intact *Torilis scabra* seeds. Vertical bars indicate ± SE with four replicates.

3.4. Effects of Temperature on Embryo Growth

The embryo length of *T. scabra* seeds under cold and warm stratification showed a slow increase during the 0–8 week incubation period (Figure 2). However, after transferring seeds incubated at 4 °C to 15/25 °C, the embryos increased rapidly, with an E/S ratio that increased from 30% to 70% two weeks after transfer. After 12 weeks of incubation, the E/S ratio increased from 0.24 (at 0 weeks) to 0.82 (at 12 weeks). In contrast, the E/S ratio of seeds remained almost unchanged after transfer from 15/25 °C to 4 °C.

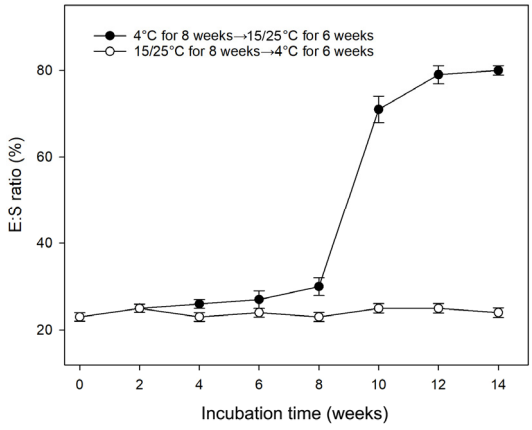

Figure 2. Effect of temperature on embryo:seed (E:S) length ratio of *Torilis scabra*. Vertical bars indicate ± SE with 10 replicates.

3.5. Effects of Cold or Warm Stratification on Seed Germination

The germination percentage increased with an increase in cold stratification period from 0 to 16 weeks at 4 °C (Figure 3). Additionally, seeds that were incubated under light conditions had a higher germination percentage compared to those in the dark (Figure 3). Seeds that were incubated at temperatures of 10/20 and 5/15 °C had a higher germination percentage compared to those incubated at 15/25 and 20/30 °C. After a 12 week incubation, 73% of the seeds germinated under light conditions at 5/15 °C, 90% at 10/20 °C, 10% at 15/25 °C, and 9% at 20/30 °C. However, under dark conditions, only 22% germinated at 5/15 °C, 33% at 10/20 °C, 4% at 15/25 °C, and 3% at 20/30 °C. On the other hand, after 16 weeks of warm stratification, no seed germination was observed after 30 days of incubation under light or dark conditions at 5/15, 10/20, 15/25, or 20/30 °C.

3.6. Effects of Warm plus Cold Stratification on Seed Germination

As revealed by three-way ANOVA, a 0–4 week warm stratification combined with a 12 week cold stratification, incubation temperature, and light significantly affected *T. scabra* seed germination. After a 4 week warm stratification combined with a 12 week cold

stratification, seeds displayed significantly higher germination percentages than seeds with a 0 week warm stratification combined with a 12 week cold stratification (Figure 4).

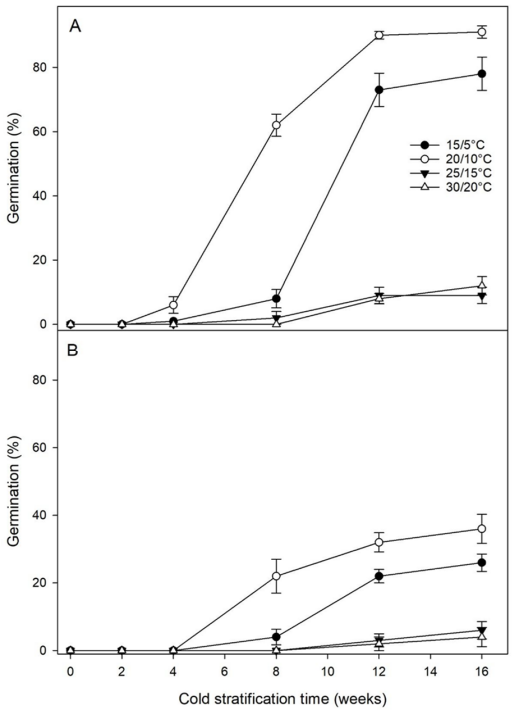

Figure 3. Effect of 16 weeks of cold stratification at 4 °C and incubation temperature at 5/15, 10/20, 15/25, and 20/30 °C on germination of *Torilis scabra* seeds under light (**A**) and darkness (**B**). Vertical bars indicate ± SE with four replicates.

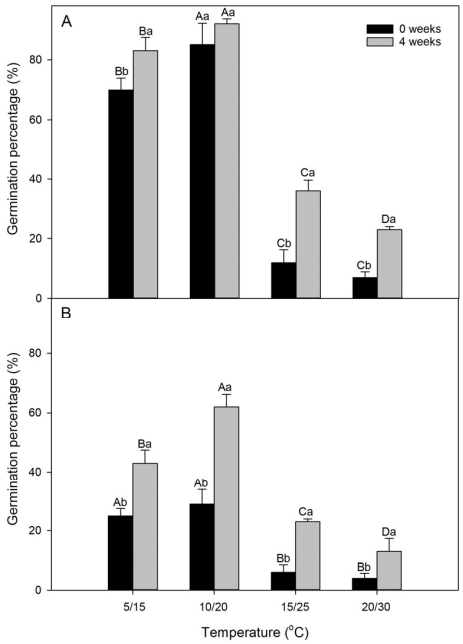

Figure 4. Effects of light (**A**) or darkness (**B**), incubation temperature (5/15, 10/20, 15/25, and 20/30 °C), and 0 or 4 weeks of warm stratification plus 12 weeks of cold stratification on germination of *Torilis scabra* seeds. Vertical bars indicate ± SE with four replicates. Significant differences between incubation temperatures for the same warm stratification period and between warm stratification periods for the same incubation temperature ($p < 0.05$) are indicated by different capital and lowercase letters, respectively.

3.7. Effects of Dry Storage (After-Ripening) on Seed Germination

Eight-week dry storage under room temperature conditions showed that the seeds did not germinate after 30 days of incubation under 5/15, 10/20, 15/25, and 20/30 °C, with or without light.

3.8. Effects of Gibberellin on Seed Germination

GA_3 concentration, incubation time, and their interaction significantly affected *T. scabra* seed germination. As the concentration of GA_3 increased from 0 to 1000 mg/L and/or the incubation time increased from 4 to 12 weeks, the seed germination percentage significantly increased (Figure 5).

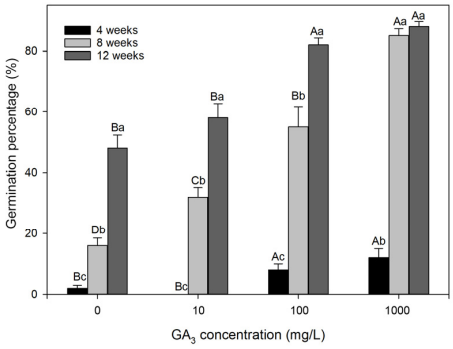

Figure 5. Effects of GA_3 concentration and incubation periods on germination of *Torilis scabra* seeds at 15/25 °C in light. Vertical bars indicate ± SE with four replicates. Significant differences between GA_3 concentrations for the same incubation period and between incubation periods for the same GA_3 concentration ($p < 0.05$) are represented by different capital and lowercase letters, respectively.

3.9. Germination Phenology and Embryo Growth

E/S ratio in fresh seeds was 0.23 ± 0.01, while before germination it was 0.69 ± 0.01 (Figure 6). The E/S ratio showed little or no increase without an increase in soil temperatures, which began after 1 February 2019 at the maximum and minimum daily temperatures of 0.2 °C and 8.3 °C, respectively (Figure 6). Seed germination was at the highest rate on 14 February 2020 at the minimum and maximum daily temperatures of 1 °C and 12 °C, respectively. By 14 March 2019, >80% seed germination percentage was observed in the soil.

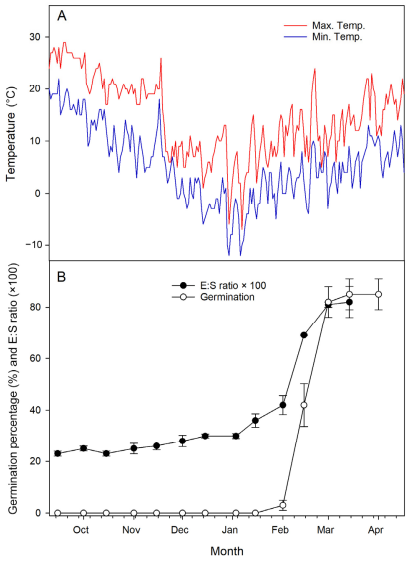

Figure 6. Mean daily maximum and minimum air temperatures (**A**), embryo:seed length ratio, and cumulative germination (**B**) of *Torilis scabra* seeds buried at a depth of 2 cm in soil were recorded from September 2018 to April 2019. Vertical bars indicate ± SE with four replicates.

4. Discussion

Physical dormancy can be distinguished by the presence of imbibition in sacrificed seeds but not in intact seeds [15]. Seeds of *T. scabra* absorbed water rapidly, as described above (Figure 1). We concluded that *T. scabra* seeds do not exhibit PY or physical dormancy + physiological dormancy. Germination of *T. scabra* fresh seeds was not observed in their natural habitat following sowing or after 1 month of laboratory experiments at 5/15, 10/20, 15/25, or 20/30 °C, indicating that they are dormant when initially dispersed. However, prior to seed germination in the field, embryo:seed length ratio increased from 0.23 ± 0.01 to 0.69 ± 0.01. Therefore, embryos of *T. scabra* seed are underdeveloped. According to Baskin and Baskin [13], MD occurs when seeds with immature embryos germinate within 30 days on a moist medium, while MPD occurs when seeds with immature embryos fail to germinate after a 30 day incubation period on a moist medium. Therefore, seeds of *T. scabra* exhibit MPD due to a lack of initial germination and because they have undeveloped embryos.

Understanding the embryo development conditions in *T. scabra* seeds is essential for categorizing the MPD level. There are nine MPD levels, which are further classified into simple and complex types according to temperatures needed for embryo development [13,38]. Seeds with simple MPD require warm temperatures (above 15 °C) for embryonic development, while those with complex MPD require low temperatures (around 0–10 °C) for embryonic development [15]. In a laboratory setting, *T. scabra* seed germination in light and darkness showed a gradual increase under 5/15, 10/20, 15/25, and 20/30 °C after increasing time for cold stratification (Figure 3). In addition, when seeds incubated at 4 °C were transferred to 15/25 °C, the embryo expanded rapidly, with an E/S ratio elevating from 30% to 70% after two weeks of transfer (Figure 2). Similarly, in the germination phenology experiments, *T. scabra* embryos remained almost unchanged prior to soil temperatures starting to increase (Figure 6). These results confirm that a requirement for cold stratification, which occurs naturally in winter, will have postponed embryo development and germination in spring in the natural habitat [35]. Because embryos in seeds of *T. scabra* were observed to grow with warm temperatures, they were classified as having simple MPD.

Nikolaeva [44] classified three PD levels, namely non-deep PD, intermediate PD, and deep PD. Seeds have non-deep or intermediate PD when GA_3 substitutes the necessity for cold/warm temperature for achieving dormancy breaking, and seeds have deep PD if GA_3 cannot replace the need for warm/cold temperatures [13,45]. Impacts of cold stratification can be mimicked with the application of GA_3 in certain species experiencing intermediate dormancy; however, this will not work for other species. Meanwhile, warm or cold stratification is necessary to overcome PD in intermediate and deep simple MPD [13,46]. *T. scabra* seed germination markedly increased as GA_3 concentration increased (Figure 5); thus, GA_3 appears to have overcome dormancy in *T. scabra* seeds. Therefore, we infer that *T. scabra* seeds experience non-deep simple MPD and that dormancy breaking requires a comparatively short cold stratification.

The conventional notation for non-deep simple MPD is C_1B_b, where "C_1" signifies non-deep PD and "B" symbolizes the immature embryo requiring warm conditions to develop [13]. There are two variations of this dormancy type, referred to as $C_{1b}B_b$ and $C_{1a}B_b$. Warm temperatures can be used to break the PD of $C_{1b}B_b$, whereas cold temperature breaks the PD of $C_{1a}B_b$. The dormancy formula for *T. scabra* seeds is $C_{1a}B_b$ because they need low temperatures to emerge from dormancy.

The dormant state of *T. scabra* seeds prevents them from sprouting following dispersal in the fall. During the winter, cold stratification breaks PD but no embryo development observed. As the temperature rises in early spring, this triggers the development of the embryo within *T. scabra* seeds, leading to successful germination. A similar germination phenology was observed in seeds of *Angelica sylvestris* collected in Belgium [19]. These seed dormancy-breaking and germination mechanisms offer optimal timing for germination and seedling emergence [47]. During winter, plants would face challenges such as low temperatures and limited water availability, which would negatively affect their growth. However, by undergoing a period of cold stratification followed by exposure to high

temperatures, the seeds are primed to germinate when conditions become favorable in the spring. This allows the plant to establish and grow at the right time, thereby increasing its chances of survival and success in the long term. We thus consider that delaying germination in this way is advantageous and avoids germination during unfavorable winter conditions.

Dormancy-breaking requirements of many Apiaceae species seeds have been widely examined [19]. Deep complex MPD [26], deep simple MPD [23], and non-deep simple MPD [17,35] have all been observed in Apiaceae seeds. In deep and non-deep complex MPD, PD breaking and embryo development happen at the same time throughout the cold stratification process. Seeds under deep simple MPD should experience warm stratification and then cold stratification for achieving germination. In certain Apiaceae seeds experiencing non-deep simple MPD, warm stratification contributes to PD breaking, as observed in *Chaerophyllum taintinurieri* [15]. Species that germinate in spring within temperate regions usually need cold stratification for PD breaking, such as *Asimina triloba* [48], *Thalictrum mirabile* [49], and *Angelica keiskei* [35]. For spring-germinating species that possess seeds with non-deep simple MPD, breaking of the PD may occur during the winter season. In this case, the seeds will be primed for germination and embryo development once favorable conditions arise in the spring. This allows the plant to establish and grow at the appropriate time, which is critical for survival and success in the long term. Such heterogeneities in dormancy strategy are possibly associated with selection in diverse habitats [29].

5. Conclusions

Seeds of *T. scabra* exhibit non-deep simple MPD, which is a combination of MD and PD. The underdeveloped embryos (i.e., MD) did not begin to grow until the PD was broken through cold stratification. Subsequently, warm temperatures increased seed germination and embryo development. Moreover, the application of GA_3 can replace cold stratification, while after-ripening is ineffective for this purpose. In the field, embryo length showed little or no increase before 1 February and germination peaked on 14 February. This study will aid the horticulture industry and efforts to conserve this species by reducing the time it takes to produce *T. scabra* seedlings, thus serving as a useful resource.

Author Contributions: L.Z. and K.Z. designed and supervised the study; H.L. conducted the field work with the help of L.Z., C.X. and J.T.; L.Z. and K.Z. wrote the first draft and various revisions of the manuscript. All authors have read and agreed to the published version of the manuscript.

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References

1. Penfield, S.; Springthorpe, V. Understanding chilling responses in *Arabidopsis* seeds and their contribution to life history. *Philos. Trans. R. Soc. B-Biol. Sci.* **2012**, *367*, 291–297. [CrossRef] [PubMed]
2. Springthorpe, V.; Penfield, S. Flowering time and seed dormancy control use external coincidence to generate life history strategy. *eLife* **2015**, *4*, e05557. [CrossRef] [PubMed]
3. Rajapakshe, R.P.; Cross, A.T.; Turner, S.R.; Tomlinson, S. Understanding the interplay of temperature and moisture on the germination niche to improve management of threatened species impacted by mining. *Restor. Ecol.* **2022**, *30*, e13708. [CrossRef]
4. Turcotte, M.M.; Levine, J.M. Phenotypic plasticity and species coexistence. *Trends Ecol. Evol.* **2016**, *31*, 803–813. [CrossRef] [PubMed]
5. James, A.R. Inter-annual facilitation via pollinator support arises with species-specific germination rates in a model of plant–pollinator communities. *Proc. R. Soc. B* **2023**, *290*, 20221485. [CrossRef]

6. Simons, A.M.; Johnston, M.O. Environmental and genetic sources of diversification in the timing of seed germination: Implications for the evolution of bet hedging. *Evolution* **2006**, *60*, 2280–2292. [CrossRef] [PubMed]
7. Mondoni, A.; Rossi, G.; Orsenigo, S.; Probert, R.J. Climate warming could shift the timing of seed germination in alpine plants. *Ann. Bot.* **2012**, *110*, 155–164. [CrossRef]
8. Tielbörger, K.; Petruů, M.; Lampei, C. Bet-hedging germination in annual plants: A sound empirical test of the theoretical foundations. *Oikos* **2012**, *121*, 1860–1868. [CrossRef]
9. Lewandrowski, W.; Erickson, T.E.; Dalziell, E.L.; Stevens, J.C. Ecological niche and bet-hedging strategies for *Triodia* (R. Br.) seed germination. *Ann. Bot.* **2018**, *121*, 367–375. [CrossRef]
10. Finch-Savage, W.E.; Footitt, S. Seed dormancy cycling and the regulation of dormancy mechanisms to time germination in variable field environments. *J. Exp. Bot.* **2017**, *68*, 843–856. [CrossRef]
11. Zhang, K.; Ji, Y.; Fu, G.; Yao, L.; Liu, H.; Tao, J.; Walck, J.L. Dormancy cycles in *Aquilegia oxysepala* Trautv. et Mey. (Ranunculaceae), a species with non-deep simple morphophysiological dormancy. *Plant Soil* **2021**, *464*, 223–235. [CrossRef]
12. Zhang, K.; Ji, Y.; Song, X.; Yao, L.; Liu, H.; Tao, J. Deep complex morphophysiological dormancy in seeds of *Clematis hexapetala* Pall. (Ranunculaceae). *Sci. Hortic.* **2021**, *286*, 110247. [CrossRef]
13. Baskin, J.M.; Baskin, C.C. The great diversity in kinds of seed dormancy: A revision of the Nikolaeva-Baskin classification system for primary seed dormancy. *Seed Sci. Res.* **2021**, *31*, 249–277. [CrossRef]
14. Martin, A.C. The comparative internal morphology of seeds. *Am. Midl. Nat.* **2013**, *36*, 531–660. [CrossRef]
15. Baskin, C.C.; Baskin, J.M. *Seeds: Ecology, Biogeography, and Evolution of Dormancy and Germination*, 2nd ed.; Academic Press: San Diego, CA, USA, 2014.
16. Baskin, J.M.; Baskin, C.C. Seed germination ecology of poison hemlock, *Conium maculatum*. *Can. J. Bot.* **1990**, *68*, 2018–2024. [CrossRef]
17. Rawnsley, R.P.; Lane, P.A.; Brown, P.H.; Groom, T. Occurrence and severity of the weeds *Anthriscus caucalis* and *Torilis nodosa* in pyrethrum. *Aust. J. Exp. Agric.* **2007**, *46*, 711–716. [CrossRef]
18. Baskin, J.M.; Baskin, C.C. A classification system for seed dormancy. *Seed Sci. Res.* **2004**, *14*, 1–16. [CrossRef]
19. Vandelook, F.; Bolle, N.; Van Assche, J.A. Seed Dormancy and germination of the European *Chaerophyllum temulum* (Apiaceae), a Member of a Trans-Atlantic Genus. *Ann. Bot.* **2007**, *100*, 233–239. [CrossRef]
20. Vandelook, F.; Van de Moer, D.; Van Assche, J.A. Environmental signals for seed germination reflect habitat adaptations in four temperate Caryophyllaceae. *Funct. Ecol.* **2008**, *22*, 470–478. [CrossRef]
21. Baskin, C.C.; Baskin, J.M.; Chester, E.W. Ecological life cycle of *Trepocarpus aethusae* (Nutt.) ex DC. and comparisons with two other winter annual apiaceae native to Eastern United States. *Castanea* **2003**, *68*, 43–55.
22. Nikolaeva, M.G.; Rasumova, M.V.; Gladkova, V.N. *Reference Book on Dormant Seed Germination*, 2nd ed.; "Nauka" Publishers (Leningrad Branch): Leningrad, Russia, 1985.
23. Rosbakh, S.; Phartyal, S.S.; Poschlod, P. Seed germination traits shape community assembly along a hydroperiod gradient. *Ann. Bot.* **2020**, *125*, 67–78. [CrossRef] [PubMed]
24. Baskin, J.M.; Baskin, C.C. Nondeep complex morphophysiological dormancy in seeds of *Osmorhiza claytonii* (Apiaceae). *Am. J. Bot.* **1991**, *78*, 588–593. [CrossRef]
25. Baskin, J.M.; Baskin, C.C. Germination ecophysiology of the woodland herb *Osmorhiza longistylis* (Umbelliferae). *Am. J. Bot.* **1984**, *71*, 687–692. [CrossRef]
26. Hawkins, T.S.; Baskin, C.C.; Baskin, J.M. Morphophysiological dormancy in seeds of three eastern North American *Sanicula* species (Apiaceae subf. Saniculoideae): Evolutionary implications for dormancy break. *Plant Species Biol.* **2010**, *25*, 103–113. [CrossRef]
27. Baker, K.S.; Steadman, K.J.; Plummer, J.A.; Merritt, D.J.; Dixon, K.W. The changing window of conditions that promotes germination of two fire ephemerals, *Actinotus leucocephalus* (Apiaceae) and *Tersonia cyathiflora* (Gyrostemonaceae). *Ann. Bot.* **2005**, *96*, 1225–1236. [CrossRef]
28. Phartyal, S.S.; Kondo, T.; Baskin, J.M.; Baskin, C.C. Temperature requirements differ for the two stages of seed dormancy break in *Aegopodium podagraria* (Apiaceae), a species with deep complex morphophysiological dormancy. *Ann. Bot.* **2009**, *96*, 1086–1095. [CrossRef]
29. Vandelook, F.; Lenaerts, J.; Jozef, A. The role of temperature in post-dispersal embryo growth and dormancy break in seeds of *Aconitum lycoctonum* L. *Flora* **2009**, *204*, 536–542. [CrossRef]
30. Baskin, C.C.; Milberg, P.; Anderson, L.; Baskin, J.M. Deep complex morphophysiological dormancy in seeds of *Anthriscus sylvestris* (Apiaceae). *Flora* **2000**, *195*, 245–251. [CrossRef]
31. Baskin, J.M.; Baskin, C.C. The ecological life cycle of *Cryptotaenia canadensis* (L.) DC. (Umbelliferae), a woodland herb with monocarpic ramets. *Am. Midl. Nat.* **1988**, *119*, 165–173. [CrossRef]
32. Schutte, B.; Knee, M. The effects of rudimentary embryos and elevated oxygen on seed dormancy of *Eryngium yuccifolium* Michx. (Apiaceae). *Seed Sci. Technol.* **2005**, *33*, 53–62. [CrossRef]
33. Nelson, J.R.; Wilson, A.M.; Goebel, C.J. Factors influencing broadcast seeding in bunchgrass range. *Rangel. Ecol. Manag.* **1970**, *23*, 163–170. [CrossRef]
34. Brooks, S.; Cordell, S.; Perry, L. Broadcast seeding as a potential tool to reestablish native species in degraded dry forest ecosystems in Hawaii. *Ecol. Restor.* **2009**, *27*, 300–305. [CrossRef]

35. Zhang, K.; Zhang, Y.; Walck, J.L.; Jun, T. Non-deep simple morphophysiological dormancy in seeds of *Angelica keiskei* (Apiaceae). *Sci. Hortic.* **2019**, *255*, 202–208. [CrossRef]
36. Yan, A.; Chen, Z. The control of seed dormancy and germination by temperature, light and nitrate. *Bot. Rev.* **2020**, *86*, 39–75. [CrossRef]
37. Kawano, H.; Kanazawa, Y.; Suzuki, K.; Ohara, M. Seed germination characteristics of *Maianthemum dilatatum* (Wood) Nels. et Macbr. (Asparagaceae). *Plant Species Biol.* **2020**, *35*, 38–48. [CrossRef]
38. Zhang, K.; Pan, H.; Baskin, C.C.; Baskin, J.M.; Xiong, Z.; Cao, W.; Yao, L.; Tang, B.; Zhang, C.; Tao, J. Epicotyl morphophysiological dormancy in seeds of *Paeonia ostii* (Paeoniaceae): Seasonal temperature regulation of germination phenology. *Environ. Exp. Bot.* **2022**, *194*, 104742. [CrossRef]
39. Hidayati, S.N.; Walck, J.L.; Taylor, J. Seed germination ecophysiology of two western North American species of *Sambucus* (Caprifoliaceae *sensu lato*), and comparisons with eastern North American and European congeners. *Plant Species Biol.* **2010**, *25*, 203–213. [CrossRef]
40. Tsang, A.C.W.; Corlett, R.T. Reproductive biology of the *Ilex* species (Aquifoliaceae) in Hong Kong, China. *Can. J. Bot.* **2005**, *83*, 1645–1654. [CrossRef]
41. She, M.; Watson, M.F. *Flora of China*, 3rd ed.; Science Press: Beijing, China; Missouri Botanical Garden Press: St. Louis, MO, USA, 2005; p. 28.
42. Ye, J. *Common Chinese Herbs in Daily Life*, 2nd ed.; People's Publishing House of Shandong: Jinan, China, 2009.
43. Zhang, Y.; Zhang, X.; Guo, T.; Luo, X. Characteristics of temperature and precipitation change and the influence on climate productive potential in the Northwestern Liaoning. *Chin. J. Agrometeorol.* **2015**, *36*, 203.
44. Nikolaeva, M.G. Factors controlling the seed dormancy pattern. In *The Physiology and Biochemistry of Seed Dormancy and Germination*, 2nd ed.; Khan, A.A., Ed.; North Holland Publishing Co.: Amsterdam, The Netherlands, 1977; pp. 51–74.
45. Lee, S.Y.; Rhie, Y.H.; Kim, K.S. Non-deep simple morphophysiological dormancy in seeds of *Thalictrum rochebrunianum*, an endemic perennial herb in the Korean Peninsula. *Hortic. Environ. Biotechnol.* **2015**, *56*, 366–375. [CrossRef]
46. Nurulla, M.; Baskin, C.C.; Lu, J.; Tan, D.; Baskin, J.M. Intermediate morphophysiological dormancy allows for life-cycle diversity in the annual weed, *Turgenia latifolia* (Apiaceae). *Aust. J. Bot.* **2014**, *62*, 630–637. [CrossRef]
47. Kang, J.; Yim, S.; Choi, H.; Kim, A.; Lee, K.P.; Lopez-Molina, L.; Martinoia, E.; Lee, Y. Abscisic acid transporters cooperate to control seed germination. *Nat. Commun.* **2014**, *6*, 8113. [CrossRef] [PubMed]
48. Geneve R, L. Impact of temperature on seed dormancy. *HortScience* **2003**, *38*, 336–340. [CrossRef]
49. Walck, J.L.; Baskin, C.C.; Baskin, J.M. Seeds of *Thalictrum mirabile* (Ranunculaceae) require cold stratification for loss of nondeep simple morphophysiological dormancy. *Can. J. Bot.* **1999**, *77*, 1769–1776. [CrossRef]