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Ecophysiology of seed dormancy and germination in four *Lonicera* (Caprifoliaceae) species native to Korea

HyungBin Park[1†], ChungHo Ko[1†], SeungYoun Lee[1,2†], SangYong Kim[1], JongCheol Yang[1] and KiCheol Lee[1*]

Abstract

Background: To exploit the ornamental and medicinal purposes of *Lonicera harae* Makino, *L. subsessilis* Rehder, *L. praeflorens* Batalin, and *L. insularis Nakai*, native to Korea, it is necessary to understand their seed ecology for propagation. In this study, we investigated the seed dormancy type and germination characteristics of seeds of the four Korean native *Lonicera* species.

Results: The seeds of the four *Lonicera* species imbibed water readily, suggesting that the species do not have physical dormancy. Furthermore, the seeds exhibited underdeveloped embryos with only about 15–25% of the length of the seeds at dispersal. The embryos grew to the critical length with approximately 50–80% of the length of the seeds' development before radicle protrusion. Further, 94.4% and 61.1% of freshly matured seeds of *L. insularis* and *L. harae* germinated within 4 weeks after sowing at 15 °C and 20 °C, respectively. Contrarily, *L. praeflorens* and *L. subsessilis* seeds did not germinate within 4 weeks under all temperature treatments. At 15 °C, *L. praeflorens* seeds started to germinate from 5 weeks and the final germination rate was 51.1% at 13 weeks. At 15 °C, *L. subsessilis* seeds started to germinate from 5 weeks after sowing and the final germination rate was 85.6% at 17 weeks after sowing. Embryo growth and germination of *L. praeflorens* and *L. subsessilis* occurred at a relatively high temperature (≥ 15 °C).

Conclusions: Overall, *L. insularis* seeds have only morphological dormancy. The seeds of *L. harae* have approximately 60% and 40% of morphological dormancy and morphophysiological dormancy, respectively. Contrarily, *L. praeflorens* and *L. subsessilis* exhibited non-deep simple-type morphophysiological dormancy that requires relatively high temperature (≥ 15 °C) for embryo growth and dormancy breaking. The optimum temperature for the germination of seeds of *L. insularis*, *L. harae*, *L. praeflorens*, and *L. subsessilis* was 15 °C, 20 °C, 15 °C, and 20 °C, respectively. There was interspecific variation in seed dormancy and germination patterns in the four *Lonicera* species. The difference in these characteristics within the four *Lonicera* species could be useful for understanding the seed ecophysiological mechanisms of *Lonicera* species.

Keywords: Ecological adaption, *Lonicera* species, Morphological dormancy, Morphophysiological dormancy, Non-deep simple morphophysiological dormancy

* Correspondence: yloml@korea.kr
†Hyung Bin Park, Chung Ho Ko and Seung Youn Lee contributed equally to this work.
[1]Division of Plant Resources, Korea National Arboretum, Yangpyeong 12519, South Korea
Full list of author information is available at the end of the article

Background

The genus *Lonicera* of the family Caprifoliaceae includes more than 200 species that are mostly arching shrubs or small trees cultivated as ornamental crops (Theis et al. 2008). *Lonicera* is mostly distributed in the Northern Hemisphere such as North America, Europe, and Asia (Naugžemys et al. 2007). Not only the plants, known as "honeysuckles," are useful resources for ornamental and medicinal purposes, but also their extracts can be used as a herbal medicine for inflammation in China (Theis et al. 2008; Ryuk et al. 2012; Yuan et al. 2012; Kim et al. 2016). There are 17 *Lonicera* species that are native to Korea (Lee 2003). Especially, *L. insularis* Nakai and *L. subsessilis* Rehder are Korean endemic plants that are distributed along the shore of Ulleungdo and from Pyeongannam-do to Jeollanam-do in Korea, respectively (Jeong et al. 2014; KNA 2019). To exploit these plant resources, investigating germination characteristics and seed dormancy type is needed.

Dormant seeds are viable seeds that do not germinate for a period of time even under environmental conditions that are favorable for germination, and thus, they can avoid unfavorable environmental conditions (Finch-Savage and Leubner-Metzger 2006). Seed dormancy is divided into the following five categories: (1) physical dormancy (PY), (2) physiological dormancy (PD), (3) morphological dormancy (MD), (4) morphophysiological dormancy (MPD), and (5) combinational dormancy (PY+PD) (Baskin and Baskin 1998). Among them, seeds with MD and MPD have underdeveloped embryos during seed dispersal (Nikolaeva 1977; Baskin and Baskin 1998).

Seeds with MD have underdeveloped embryo and these seeds are not physiologically dormant (Baskin and Baskin 1998). Embryo of the seeds with MD must grow to a critical length before radicle protrusion. However, the seeds with MD do not require pretreatments for dormancy breaking; they only need time to grow full-sized embryo before radicle protrusion (Baskin and Baskin 2004a). Morphophysiological dormancy is a combination of MD and PD. Thus, MPD require time not only to grow embryo to a critical size, but also to break PD by cold and/or warm stratification. Morphophysiological dormancy in seeds is classified into eight types according to requirements of environmental conditions for seed dormancy breaking and embryo growth and germination responses to gibberellic acid (Baskin and Baskin 2004a).

From an ecological perspective, seed dormancy plays an important role in how germination timing is controlled in a natural habitat and how plants adapt to their natural environments (Geneve 2003). Thus, seed dormancy and germination requirements can provide insights into how plants determine where they can grow (Santiago et al. 2012). Furthermore, because the type of seed dormancy varies within the genus and species, classification of seed dormancy type among species in the same genus provides insights into how each species adapts to different natural habitats. In a previous study, the seeds of four *Lonicera* species native to North America were investigated to classify seed dormancy type (Hidayati et al. 2000b). The seeds of these species had MPD or MD or a combination of MD and MPD. *Lonicera caerulea* var. *emphyllocalyx* has only MD (Phartyal et al. 2009). On the contrary, *L. fragrantissima* has deep simple MPD and *L. japonica* has non-deep simple MPD (Baskin and Baskin 1998). Half of the seeds of *L. maackii* and *L. morrowii* have MD and the other half has non-deep simple MPD (Hidayati et al. 2000b; Santiago et al. 2012). However, seed dormancy and germination characteristics of Korean native *Lonicera* species have not been studied. The aim of the present study was to investigate seed dormancy type and germination characteristics of four *Lonicera* species native to Korea. These results will be useful to understand seed ecology and to identify optimum temperature treatments for propagating these *Lonicera* species.

Materials and methods

Seed source

To investigate the seed dormancy type and germination characteristics of the four *Lonicera* species, the fruits of these species were collected from 2016 to 2017. The seeds of *L. insularis* were collected in June 2016 from plants growing in Ulleungdo, Korea. The seeds of *L. subsessilis* Rehder were collected in September 2016 from plants growing in the Korea National Arboratum, Pocheon, Korea. The seeds of *L. harae* Makino and *L. praeflorens* Batalin were collected in May 2017 from plants growing in the Korea National Arboratum, Pocheon, Korea. The seeds were removed from the pulp and dried at ambient room temperature (approximately 25 °C) for 1–2 weeks, packed and sealed plastic containers, and stored at 4 °C until further analyses.

Water imbibition test

To investigate the PY of the seeds, a water imbibition test was conducted on March 4, 2018. Three replicates of 20 seeds each were used. The dry matter of the seeds was measured, and then the seeds were placed in 9-cm-diameter Petri dishes (Cell Culture Dish; SPL Life Sciences Co., Ltd., Gyeonggi-do, Korea) with two layers of filter papers (Whatman No.2; GE Healthcare, Buckinghamshire, UK) moistened with distilled water. The seeds were incubated at room temperature (approximately 25 °C). The fresh weight of seeds was measured after 3, 6, 9, 12, 24, and 48 h of incubation. The water uptake by seeds was calculated using the water uptake formula (Baskin et al. 2004b).

Water absorption (%) = $[(W_2 - W_1)/W_1] \times 100$

where, W_2 is the mass of the seeds after imbibition for a given interval and W_1 is the initial seed mass.

Seed morphology

To investigate MD, the seed morphology measurement was carried out on April 5, 2018 to June 12, 2018. The seeds of *L. insularis* and *L. praeflorens* were incubated at 15 °C, whereas the seeds of *L. harae* and *L. subsessilis* were incubated at 20 °C. The seeds were halved using a razor blade (stainless blade; Dorco, Seoul, KR), and then the length of the embryo of the seeds at dispersal and just before germination was measured using a USB microscope (AM 3111 Dino-Lite Premier; AnMo Electronics Co., Taiwan). Thereafter, the embryo/seed ratio (E:S ratio) was calculated and compared between seed dispersal and just before germination.

Temperature treatments

To investigate the seed dormancy type and optimum temperatures for germination, temperature experiments were carried out from May 25, 2017, to December 8, 2017. Three replicates with 30 seeds were used. The seeds were placed on two sheets of filter papers moistened with distilled water in 9-cm-diameter Petri dishes. All Petri dishes were sealed with Parafilm (PM-996; Bemis Company Inc., USA) to reduce water loss during incubation. Temperature and light-controlled multi-room chambers (WIM-R L4; Daihan scientific Co. Ltd., Wonju, Korea) were used in this experiment. The growth chambers were set at constant temperatures of 5 °C, 15 °C, 20 °C and 25 °C and 12-h light/dark photoperiod using cool white fluorescent lamps, producing a photon flux density of approximately 15–20 $\mu mol^{-2}\ s^{-1}$.

For *L. subsessilis*, seasonal temperature cycling treatment known as move-along experiment was performed from May 25, 2017 to February 10, 2018 (Baskin and Baskin 2003). In the move-along experiment, one set (move A treatment) of seeds was placed at 5 °C. After 12 weeks, they were moved from 5 °C to 15 °C (4 weeks) → 20 °C (4 weeks) → 25 °C (12 weeks). The second set (move B treatment) of seeds was placed initially at 25 °C. After 12 weeks, they were moved from 25 °C to 20 °C (4 weeks) → 15 °C (4 weeks) → 5 °C (12 weeks). The germinated seeds were counted every week and removed from the Petri dishes. Sterilized water was frequently supplied to the Petri dishes to maintain moist condition. Rotten seeds were removed and excluded from the calculation of germination rate.

Statistical analysis

Statistical Analysis System (SAS) version 9.4 (SAS Institute Inc., Cary, NC, USA) was used for statistical analyses of the data. Differences between the mean final germination rate of seed under four temperature treatments were assessed using Tukey's honestly significant difference tests. Differences between the E:S ratio of seeds at seed dispersal and just before germination were assessed using paired t tests. The results with p values < 0.05 were considered statistically significant.

Results

Water imbibition test

The mass of the seeds of *L. insularis*, *L. harae*, *L. praeflorens*, and *L. subsessilis* was increased by approximately 50%, 90%, 35%, and 40% after 3 h of water imbibition and more than 60%, 170%, 50%, and 70% after 48 h of water imbibition, respectively (Fig. 1).

Seed morphology

The seeds of the four *Lonicera* species has undeveloped embryo at dispersal (Table 1). The E:S ratio of the seeds of *L. insularis*, *L. praeflorens*, *L. harae*, and *L. subsessilis* at dispersal was 0.26 ± 0.02, 0.13 ± 0.07, 0.14 ± 0.01, and 0.16 ± 0.01 mm, respectively. The E:S ratio of the seeds of the four *Lonicera* species just before germination was 0.82 ± 0.04, 0.81 ± 0.02, 0.46 ± 0.13, and 0.74 ± 0.01 mm, respectively (Fig. 4).

Temperature treatments

The seeds of the four *Lonicera* species presented different germination characteristics under the four temperature treatments (Fig. 2). The seeds of the four *Lonicera* species did not germinate at 5 °C. At 15 °C, the freshly matured seeds of *L. insularis* and *L. harae* germinated to 94.4% and 61.1% at 4 weeks after sowing, respectively. The final germination rate of the seeds of *L. harae* was 81.1% at 23 weeks after sowing at 15 °C (Fig. 2). On the contrary, the seeds of *L. praeflorens* and *L. subsessilis* did not germinate at the four temperature regimes within 4 weeks after sowing at all temperature regimes. At 15 °C, the seeds of *L. pareflorens* and *L. subsessilis* started to germinate from 5 weeks after sowing and the final germination rate of the seeds was 51.1% and 80.0% at 13 and 17 weeks after sowing, respectively (Fig. 2). At 20 °C, the seeds of *L. insularis* and *L. harae* germinated to 88.9% and 61.1% at 4 weeks after sowing, respectively, and the final germination rate of *L. harae* was 97.8% at 16 weeks after sowing (Fig. 2). At 20 °C, the seeds *of L. praeflorens* and *L. subsessilis* started to germinate from 8 and 9 weeks after sowing, respectively, and the final germination rate of the seeds was 40.0% and 85.6% at 19 and 14 weeks after sowing, respectively (Fig. 2). At 25 °C, the final germination rate of *L. insularis*, *L. harae*, and *L. subsessilis* was 73.3%, 67.8%, and 76.7% at 9, 27, and 27 weeks after sowing, respectively. Contrarily, the seeds of *L. praeflorens* did not germinate at 25 °C during incubation (Fig. 2).

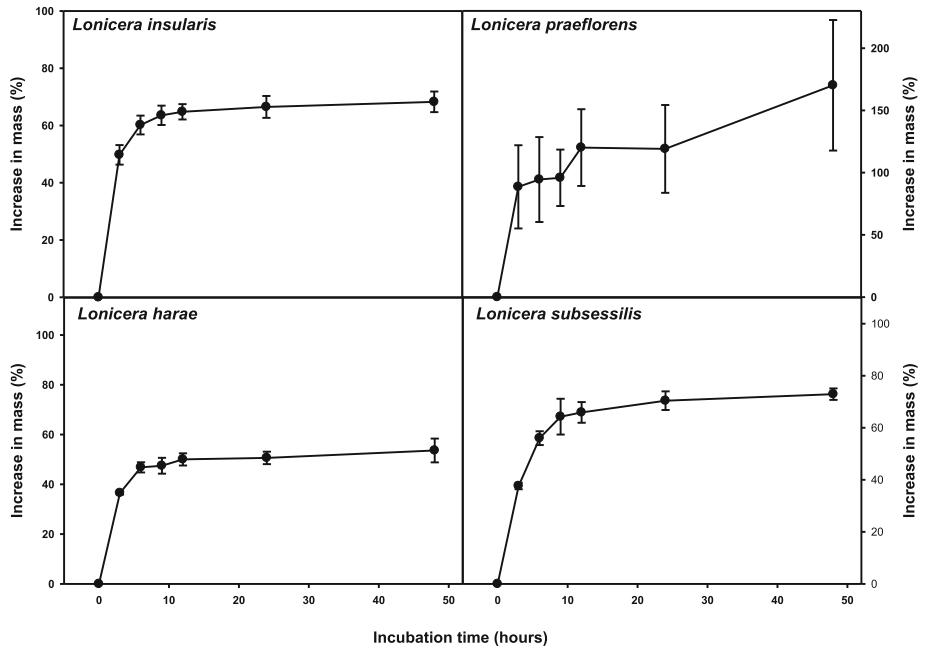


Fig. 1 Water uptake by intact seeds of *Lonicera insularis* Nakai, *Lonicera praeflorens* Batalin, *Lonicera harae* Makino, and *Lonicera subsessilis* Rehder with increase in mass. Seeds were incubated at ambient room temperature (approximately 25 °C) on filter papers moistened with distilled water for 48 h. The vertical error bars represent SE ($n = 3$)

Move-along experiments

In the move-along experiment of *L. subsessilis*, the seeds of move A treatment (start of winter) did not germinate until 24 weeks after sowing. Germination was initiated from 5 weeks after moving the seeds from 20 °C to 25 °C, and the final germination rate of the seeds was 74.4% at 29 weeks after sowing (Fig. 3). The seeds of move B treatment (start of summer) started to germinate from 3 weeks after moving the seeds from 25 °C to 20 °C, and the final germination rate of the seeds was 83.3% at 16 weeks after sowing. The final germination rate of the seeds of move B treatment was higher than that of the seeds of move A treatment (Fig. 3).

Discussion

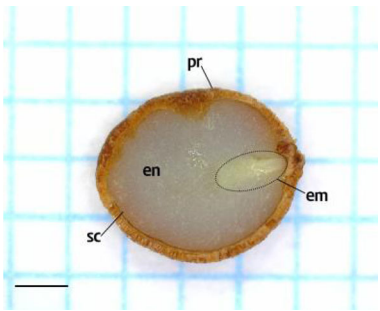
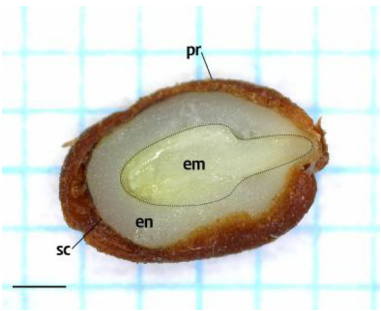
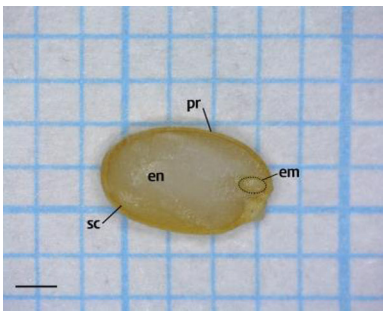
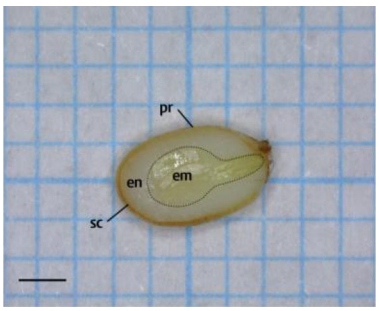
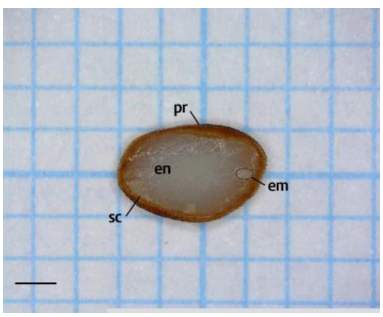
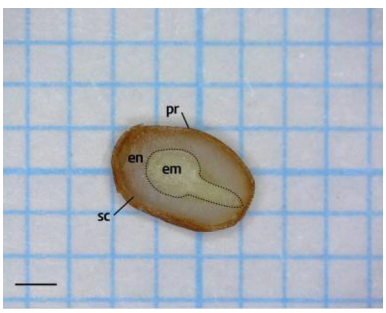
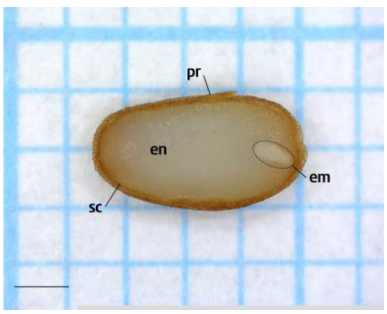
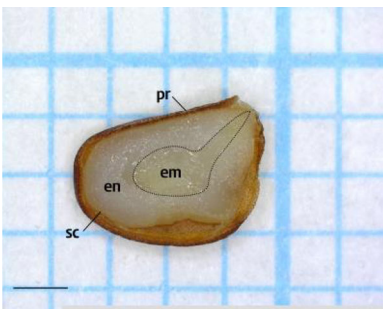
In general, the germination of seeds with PY is prevented by water impermeability of the seeds or fruit coats due to the presence of water-impermeable palisade layers of cells (Baskin and Baskin 2004b). If the mass of seeds increases to ≤ 20% in the water imbibition test, the seeds are considered impermeable to water (Baskin and Baskin 2003). This dormancy can be broken by mechanical or chemical scarification such as dry heating, dipping in boiling water, and treating with sulfuric acid (Baskin et al. 2004; Finch-Savage and Leubner-Metzger 2006; De Souza et al. 2012). In the present study, the seeds of the four *Lonicera* species imbibed water readily, suggesting that the species have no PY.

Several previous studies have reported that the seeds of *Lonicera* species have undeveloped embryo at dispersal (Martin 1946; Hidayati et al. 2000a; Hidayati et al. 2000b). In this study, we found that the embryo of the four *Lonicera* species was small and undeveloped, and they grew to the critical length before radicle protrusion. In general, underdeveloped embryo requires time to grow to the critical length. This indicates that the seeds of the species have MD or MPD (Baskin and Baskin 1998; Baskin and Baskin 2004b).

According to Baskin and Baskin (2004b), seeds with MD germinate within about 30 days. Thus, the seeds of *L. insularis* have only MD. On the contrary, approximately 60% and 40% of the seeds of *L. harae* exhibited MD and MPD, respectively. In the case of *L. praeflorens*, the germination of seeds was initiated at a relatively high temperature (15 °C) from 5 weeks after sowing. At a high temperature (25 °C), the seeds of *L. praeflorens* did not germinate during incubation. At 15 °C, the seeds of *L. subsessilis* started to germinate from 5 weeks after sowing and the final germination rate was 80.0% at 17 weeks after sowing. At 20 °C, the seeds started to germinate from 9 weeks after sowing and the final germination rate was 85.6% at 14 weeks after sowing. The seeds of *L. praeflorens* and *L. subsessilis* did not germinate within 4 weeks after sowing (Fig. 2). Thus, the seeds of these two species have MPD.

Morphophysiological dormancy is subdivided into eight types (Nikolaeva 1977; Baskin and Baskin 1998;

Table 1 Internal seed morphology of four *Lonicera* species native to Korea. Undeveloped embryos at dispersal and fully developed embryos just before germination are shown. *pr* pericarp, *sc* seed coat, *en* endosperm, *em* embryo. Scale bars represent 1 mm

Species	Seed morphology	
	At dispersal	Just before germination
Lonicera insularis Nakai		
Lonicera praeflorens Batalin		
Lonicera harae Makino		
Lonicera subsessilis Rehder		

Walck et al. 2002; Baskin and Baskin 2004b). It is broadly divided into the following two categories: (1) simple-type MPD that requires relatively high temperature (≥ 15 °C) for embryo growth and (2) complex-type MPD that requires only low temperature (0–10 °C) for embryo growth (Baskin and Baskin 1998; Hidayati et al. 2000b). The simple and complex MPD can be sub-divided based on the level of PD: non-deep, intermediate, and deep. Non-deep simple MPD requires warm or cold stratification to break dormancy. Intermediate and deep simple MPD require warm stratification followed by cold stratification to break PD (Nikolaeva 1977; Baskin and Baskin 1998; Hidayati et al. 2000b). In a previous study, *L. fragrantissima*, *L. japonica*, *L. maackii*, and *L. morrowii* have been reported to have MPD. *L. fragrantissima* had deep simple MPD and required warm plus cold stratification to break PD. *L. japonica*, *L. maackii*, and *L. morrowii* had non-deep simple

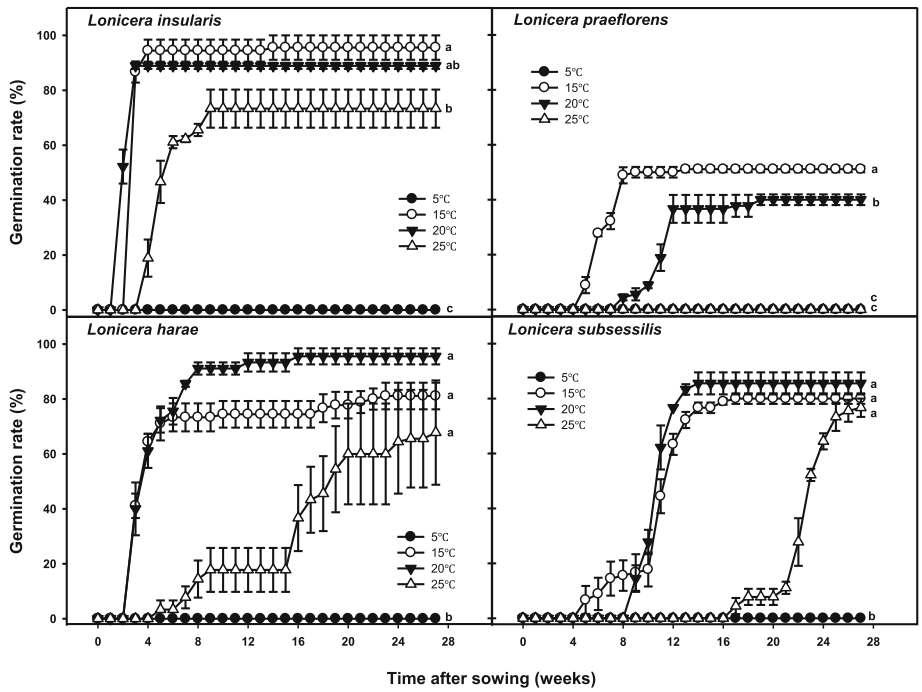


Fig. 2 Cumulative germination percentage in seeds of *Lonicera insularis* Nakai, *Lonicera praeflorens* Batalin, *Lonicera harae* Makino, and *Lonicera subsessilis* Rehder at four constant temperatures (5 °C, 15 °C, 20 °C, and 25 °C). The vertical error bars represent SE ($n = 3$). The different letters represent statistically significant differences, as determined by Tukey's HSD tests ($p < 0.05$)

MPD that required stratification (warm or cold) to break PD, in which about 50% of the seeds of *L. maackii* and *L. morrowii* had only MD (Hidayati et al. 2000b). Approximately 50% of the seeds of *L. praeflorens* require only relatively high temperature (15 °C) to grow embryo and germinate without cold stratification, whereas approximately 50% did not germinate during the experiment. Thus, approximately 50% of the seeds of *L. praeflorens* is estimated to have non-deep simple-type MPD. Because approximately 50% of the seeds of *L. praeflorens* did not germinate in this study, further studies are needed to accurately classify dormancy type in ungerminated seeds. Germination and embryo growth of *L. subsessilis* seeds occurred only at relatively high temperature (≥ 15 °C) without cold stratification. In the move-along experiment, the seeds of *L. subsessilis* germinated from 3 weeks after moving them from 25 to 20 °C in move B treatment (start of summer), whereas the seeds in move A treatment (start of winter) germinated from 5 weeks after moving them from 20 to 25 °C. The result of move B treatment was similar to that at 25 °C (Fig. 3). The seeds of move A treatment did not germinate until 12 weeks after sowing at 5 °C, and the seeds started to germinate after exposure to relatively high temperature. Thus, 85.6% of *L. subsessilis* seeds is also considered to have non-deep simple MPD. The seeds of the four *Lonicera* species showed a variation in time to germination. Various states of dormancy within the same seed population result in a slow germination rate which is an ecologically advantageous strategy for unpredictable environmental conditions (Doussi and Thanos 2002).

In a previous study, the dispersal pattern of four *Lonicera* seeds corresponded with their dormancy and germination patterns (Hidayati et al. 2000b). The seeds of *L. insularis* are dispersed from late July to August (late summer) in the natural environment. In the present study, they were exposed to temperatures that are considered optimum (15–20 °C) for germination. Because the dispersed seeds have only MD, they will germinate within 30 days after dispersal; however, if the seeds are dispersed under high temperature conditions (≥ 25 °C), their germination will be delayed. The seeds of *L. harae* are dispersed from June. When the seeds are exposed to relatively high temperature (20 °C), which was considered optimum for germination in this study, approximately 60% of the seeds will germinate within 30 days after dispersal as they have approximately 60% MD and the remaining will germinate within 16 weeks. The seeds of *L. praeflorens* begin to disperse from June, and then they are exposed to warm stratification. Because the optimum temperature to germinate is 15 °C, than 20 °C, germination of the dispersed seeds can be delayed. The seeds of *L. subsessilis* are dispersed from late September

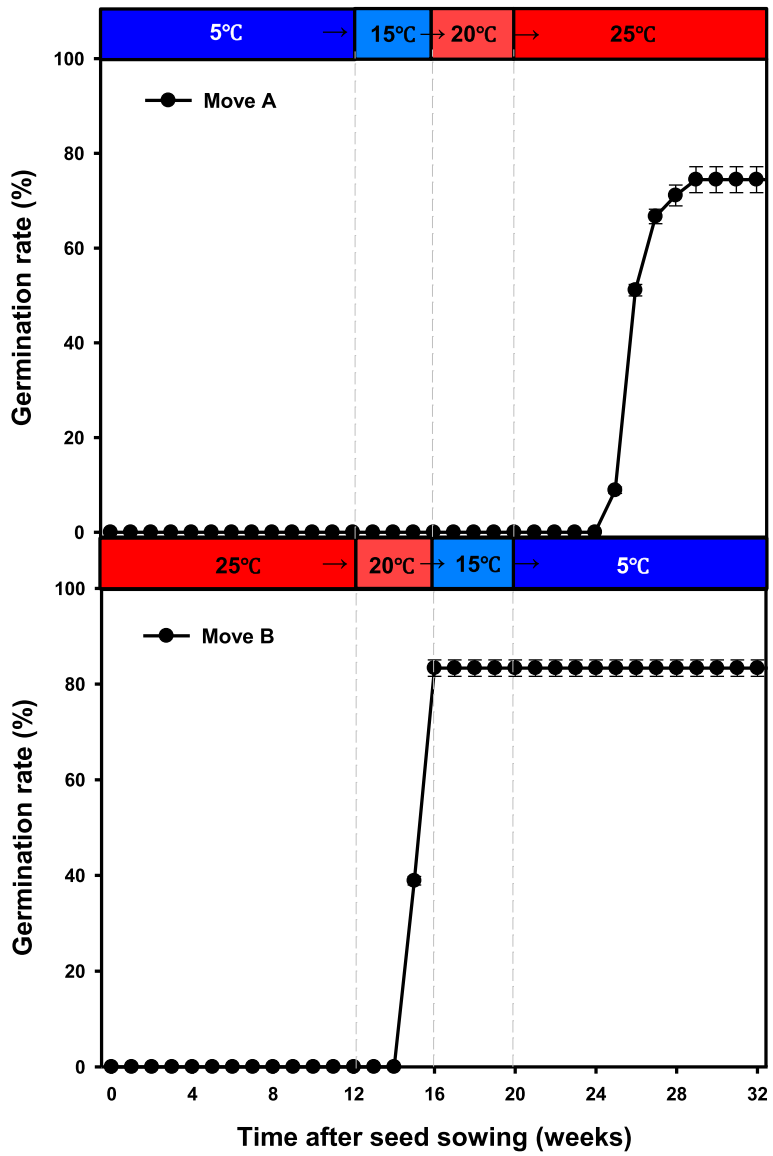


Fig. 3 Cumulative germination rate of *Lonicera subsessilis* Rehder seeds in the move-along experiment. Move A started at 5 °C (5 °C (12 weeks) → 15 °C (4 weeks) → 20 °C (4 weeks) → 25 °C (12 weeks)). Move B started at 25 °C (25 °C (12 weeks) → 20 °C (4 weeks) → 15 °C (4 weeks) → 5 °C (12 weeks)). The vertical bars represent SE ($n = 3$)

to early October (in autumn). They might be exposed to relatively high temperatures before germination. Thus, they will germinate via exposure to relatively high temperature (≥ 15 °C) in the early autumn. If they are exposed to low temperatures, germination will be delayed until they are exposed to a relatively high temperature (≥ 15 °C), as evidenced in seeds of the move A treatment (start of winter) in the move-along experiment.

In the same genus and species, seed dormancy can vary according to the native habitat (Hidayati et al. 2000a). There was stasis of ecophysiological traits such as seed dormancy and germination and ecological divergence in seed dormancy and germination characteristics of the disjunct species of the genera *Viburnum* and *Siphisia* (Adams et al. 2005; Walck et al. 2012). The disjunct species *Osmorhiza* and *Erythronium* have different seed dormancy. *Osmorhiza chilensis*, *Osmorhiza occidentalis*, and *Erythronium grandiflorum* have deep complex MPD, whereas *Osmorhiza longistylis*, *Osmorhiza claytonii*, *Erythronium albidum*, and *Erythronium americanum* have non-deep complex MPD (Baskin and Baskin 1984; Baskin and Baskin 1991; Baskin et al. 1995) . In the present study, the four *Lonicera* species exhibited common morphological traits such as undeveloped embryo. However, there was ecological divergence in seed dormancy and germination characteristics.

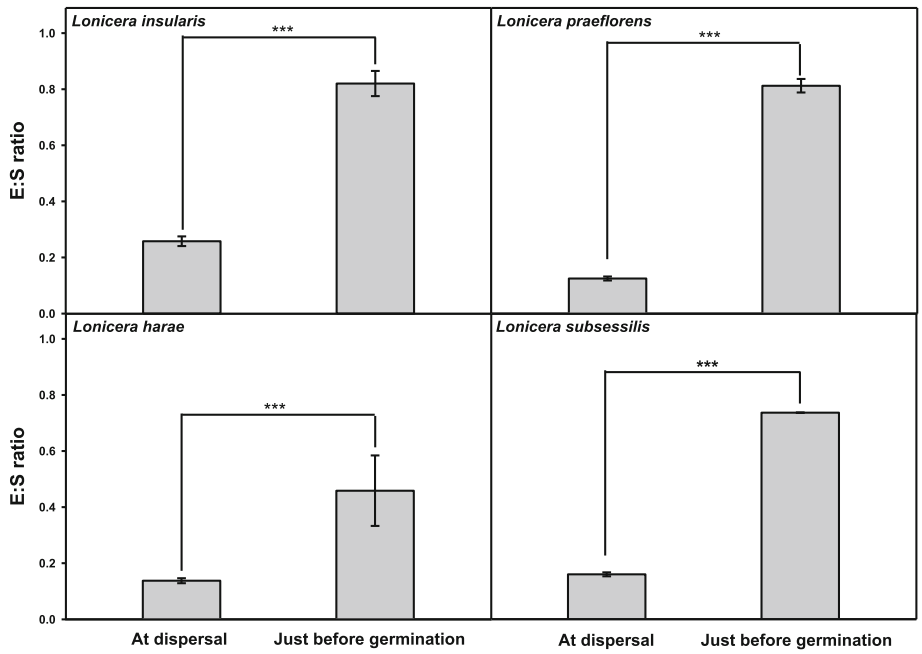


Fig. 4 Embryo/seed ratio (E:S ratio) in the seeds of *Lonicera insularis* Nakai, *Lonicera praeflorens* Batalin, *Lonicera harae* Makino, and *Lonicera subsessilis* Rehder at seed dispersal and at just before germination. The seeds of *L. insularis*, *L. praeflorens*, *L. harae*, and *L. subsessilis* were incubated at 15 °C, 15 °C, 20 °C, and 25 °C, respectively. The vertical error bars represent SE ($n = 3$). Each E:S ratio at dispersal and just before germination was compared using paired *t* test. ***$p < 0.001$

Conclusion

The results of this study revealed that the seeds of *L. insularis* have only MD and the seeds of *L. harae* have approximately 60% MD and 40% MPD. On the contrary, the seeds of *L. praeflorens* and *L. subsessilis* have non-deep simple-type MPD that requires only relatively high temperature (≥ 15 °C) for embryo growth and dormancy breaking. The optimum temperature for the germination of seeds of *L. insularis*, *L. harae*, *L. praeflorens*, and *L. subsessilis* was 15 °C, 20 °C, 15 °C, and 20 °C, respectively (Fig. 4). There was interspecific variation in seed dormancy and germination in the four *Lonicera* species. Our results will be useful for understanding seed ecophysiological mechanisms in a habitat and propagating *Lonicera* species.

Abbreviations

E:S ratio: Embryo/seed ratio; MD: Morphological dormancy; MPD: Morphophysiological dormancy; PD: Physiological dormancy; PY: Physical dormancy

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Authors' contributions

PHB, GCH, and LSY analyzed the data and wrote the manuscript. LKC designed the study and analyzed the data. YJC and KSY designed the study and coordinated the overall research. All authors read and approved the final manuscript.

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Availability of data and materials

The datasets used and/or analyzed in the present study are available from Author 1 (phb1274@ korea.kr) on reasonable request.

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

Author details

[1]Division of Plant Resources, Korea National Arboretum, Yangpyeong 12519, South Korea. [2]Division of Horticulture & Medicinal Plant, Andong National University, Andong 36729, South Korea.

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