RESEARCH REPORT



Seed dormancy and germination in *Oenanthe stolonifera* as affected by temperature and gibberellic acid

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Abstract

Our aim was to investigate the dormancy type of water dropwort seeds for developing seed germination methods in the future. The mature fruit is a schizocarp with sponge-like and thickened ribs. However, the seeds were able to absorb moisture normally. In this study, less than 14% of seeds germinated without any pretreatment after 4 weeks at 20, 25, or 25/15 °C (12/12 h). However, there was a further increase in germination percentage after 10 weeks of incubation at 5/5, 15/6, 20/10, and 25/15 °C. The seeds germinated at higher ratios under relatively colder temperature regimes. Embryo growth in the seeds occurred at both warm and cold temperatures. However, water dropwort seeds require a period of cold temperatures for embryo growth to be completed. The germination percentage was significantly higher in GA₃-treated seeds, even though the absolute difference was relatively low. In water dropwort, GA can overcome seed dormancy but cold temperature alone for 8–10 weeks may effectively break seed dormancy and increase germination percentage. Based on these results, we propose that most water dropwort seeds showed intermediate complex morphophysiological dormancy and some seeds had morphological dormancy at the time of dispersal. These results provide useful information for seed propagation and a practical production plan for cultivation of water dropwort.

Keywords Morphophysiological dormancy · Optimum germination temperature · Propagation · Seed dormancy type · Water dropwort

1 Introduction

The water dropwort (*Oenanthe stolonifera*) is widely distributed, edible and cultivable in the subantarctic regions of Korea, China, and Japan, and in the tropical regions as a perennial herb (Yang et al. 1989). In Korea, the fresh stems and leaves with a distinctive aroma and taste are used as a food (salad or seasoning in soups and stews) or as a folk medicine for the treatment of hypertension, fever, and jaundice (Whang et al. 1999; Kim et al. 2013). Kim et al. (2011)

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demonstrated that the proliferation of human hepatoma HepG2 cells was significantly inhibited by extracts of *O. stolonifera*. In recent years, the extracts of *O. stolonifera* have been made into a variety of food products in Korea (An 2014; Seo et al. 2011). Since *O. stolonifera* is commercially grown for markets, it is necessary to provide a proper growing support system ensuring adequate growth of stems and leaves for marketability.

Oenanthe stolonifera is cultivated predominantly in shallow water reservoirs or paddy lands with standing water (submerged cultivation) in South Korea. This type of cultivation is easily damaged by pests, and difficult to keep fresh and clean after harvest (Kwon et al. 2016). About 60% of the production cost is spent cleaning shoots and leaves when harvesting by conventional cultivation. In order to make up for the shortcomings of conventional submerged cultivation, some growers are trying to cultivate them in greenhouses, but the cultivation area is highly insufficient to meet overall demand in Korea. Hydroponic cultivation with plug seedlings is an alternative to labor-intensive submerged cultivation. Hydroponic cultivation is advantageous for producing

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clean product and various byproducts of *O. stolonifera* such as sprout vegetables. Thus, seed propagation of *O. stolonifera* is a necessary prerequisite for producing plug seedlings for hydroponic cultivation year round (Bae and Na 2015).

O. stolonifera seeds are known to be dormant because they rarely germinate when sown without pretreatment (Kim et al. 1987a). They have an underdeveloped embryo and a germination percentage of less than 25% (Kim et al. 1987b). Baskin and Baskin (1998) classified seed dormancy into 5 types, physiological (PD), morphological (MD), morphophysiological (MPD), physical (PY), and combinational dormancy (PY+PD). Depending on the specific seed, germination within 30 days under favorable conditions usually means seeds containing an underdeveloped embryo have either MD or MPD. Eight types of MPD have been categorized based on the temperature required for breaking seed dormancy and embryo elongation, and the response to GA. The germination percentage of O. stolonifera seeds increased as the duration of low temperatures and wet conditions increased (Kim et al. 1987a). However, in previous studies, O. stolonifera seeds showed a germination percentage of more than 60% just by simple washing treatment (Kim et al. 1987b), whereas according to Kim et al. (1987a), the germination should be preceded by at least 5 months of low-temperature and wet conditions.

Understanding seed dormancy characteristics is critical to successful mass propagation. Although there is some information on the germination of *O. stolonifera* seeds and it has been studied for various seeds grown in specific areas (different genetic lines), there are conflicting results in treatments for promoting seed germination in previous researches. Therefore, a more rigorous and detailed study is needed to determine the factors controlling germination in this species. To provide useful information for developing effective methods of *O. stolonifera* seed germination in the future, the present study focuses on determining the dormancy characteristics and the temperature requirements for germination and embryo growth of *O. stolonifera* seeds. The morphological characteristics and effects of GA on germination were also investigated to define the dormancy type.

2 Materials and methods

2.1 Seed material

Oenanthe stolonifera (inbred line, IT232354) seeds were supported by National Agrobiodiversity Center. They were cultivated and harvested from the farm of Mokpo National University, Muan, Korea in Oct. 2015, when seeds started to detach from the plant. Seeds were air-dried at room temperature (22–25 °C) for 3 d and then stored in sealed plastic jars at 5 °C.

2.2 Seed morphological characteristics and water imbibition

A dissecting microscope (Olympus SZ61, Olympus, Tokyo, Japan) was used to observe seed morphology. Seeds were cut transversely or longitudinally with a razor blade to observe the embryo.

To determine if seeds have PY, five replicates of 30 seeds were placed on filter paper (Whatman No. 2) moistened with distilled water in 9-cm Petri dishes at 20 °C. Seeds were weighed and then were placed back on Petri dishes at 0, 3, 6, 9, 12, or 24 h. Percentage water uptake (%W_s) was calculated as %W_s = [(W_g - W_i)/W_i] × 100, where W_s = increase in mass of seeds, W_i = initial mass of seeds, and W_g = mass of seeds after a given period on the wet substrate.

2.3 Effect of temperature on germination and embryo

To determine if seeds exhibit MD or MPD, seeds were incubated at a constant 5, 10, 15, 20, or 25 °C in a multi-room incubator (JSMI-02CPL, JS Research Inc., Gongju, South Korea). Germinated seeds were recorded at 1-week intervals for 12 weeks. Each experimental treatment used 100 seeds, with two replications per treatment.

To identify the temperature of dormancy breaking, temperature treatments were set: 1) alternating temperature at 5/5, 15/6, 20/10, and 25/15 °C (12/12 h); 2) temperature sequence 1: 5 °C for 12 weeks \rightarrow 15/6 °C for 4 weeks \rightarrow 20/10 °C for 2 weeks; 3) temperature sequence 2: 25/15 °C for 12 weeks \rightarrow 20/10 °C for 4 weeks \rightarrow 15/6 °C for 2 weeks. Each experimental treatment used 50 seeds, with three replications per treatment. All seeds were placed in 9-cm diameter plastic Petri dishes lined with two layers of filter paper (Whatman No. 2). Petri dishes were moistened with distilled water and sealed with parafilm (Pechiney Plastic Packaging, Menasha, WI, USA) to maintain moisture during incubation. Experiments were conducted with a 12-h photoperiod (20 μ mol m⁻² s⁻¹) by fluorescent lamps (FCL32SD/30, Kumho Electric, INC., Seoul, South Korea). A seed was considered to be germinated when the radicle or shoot protruded through the seed coat (≥ 1 mm).

For embryo growth, seeds were incubated at 5 or 25/15 °C (12/12 h) and then 30 seeds were removed at random at 1-week intervals for 12 weeks. Seeds were cut in half under a dissecting microscope using a razor blade, and the embryo length was measured with an ocular micrometer. Seed germination conditions at both temperatures were as described above.

2.4 Effects of GA₃ treatment on seed germination

Seeds were soaked in solutions of 0 (distilled water), 10, 100, 300, or 500 mg L^{-1} GA₃ at a constant temperature of 20 °C for 24 h. After soaking, seeds were washed several times with tap water and then germinated at 5 or 25/15 °C (12/12 h). Each experimental treatment used 50 seeds with five replications per treatment. Seed germination conditions were as described in 2.3 experiment.

2.5 Data collection and analysis

Data were subjected to Tukey's studentized range test or Fisher's protected least significant difference (LSD) test. For data with two comparisons, the student *t* test was used to analyze the statistical significance. A *p* value ≤ 0.05 was considered to indicate a statistically significant result. Statistical analysis was performed using SAS version 9.2 (SAS Institute Inc., Cary, NC, USA) and SPSS for Windows (IBM Corporation, New York, USA). Graph module analyses were performed using Sigma Plot software version 10.0 (SPSS Inc., Chicago, IL, USA).

3 Results

3.1 Seed morphological characteristics and water imbibition

The mature fruit is a schizocarp, which is a 2-seed fruit that splits into two mericarps (Fig. 1A, B). The fruits of *O. stolonifera* are roundish in the dorsal plane and flattened in ventral plane. The 1-seeded mericarps are dispersed separately. The seed has 4 oil canals between the primary ribs on the dorsal side and 2 canals on the ventral side (Fig. 1A–C). These glands are a dark brown color. Fruits of *O. stolonifera* have sponge-like and thickened ribs (Fig. 1A, D). The length of seeds is on average 1.57 cm (data not shown). The embryo is linear and immature (Fig. 1D). The embryo size is on average 0.25 cm long and constitutes 1/4 of the seed (data not shown).

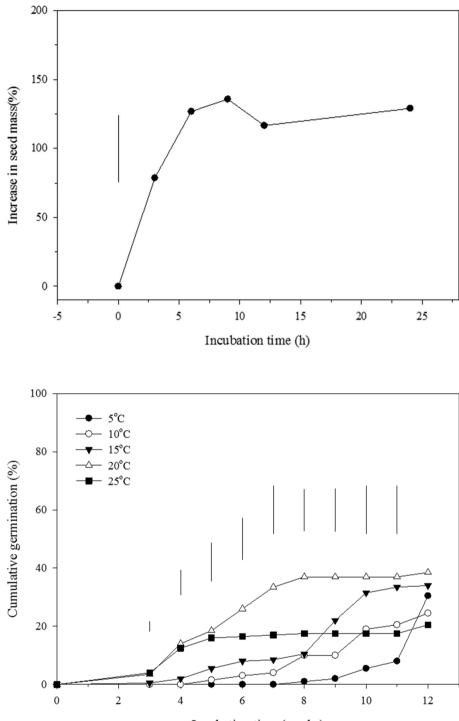
Seeds of *O. stolonifera* imbibed water and showed a typical pattern of initial rapid water uptake with the seed mass increasing by $135 \pm 10\%$ at 9 h (Fig. 2). After this point, the rate of increase in seed moisture content decreases. The seed mass was slightly decreased but was not significantly different.

3.2 Effect of temperature on germination and embryo

Seeds began to germinate after 3, 5, or 9 weeks of incubation at 20–25, 10–15, or 5 °C, respectively (Fig. 3). The

Fig. 1 Mericarps (\mathbf{a}, \mathbf{b}) and cross-sections (\mathbf{c}, \mathbf{d}) of *Oenanthe stolonifera* seeds. E, embryo; EN, endosperm; O, oil canal. Scale bar=1 mm

Fig. 2 Increase in seed mass of *Oenanthe stolonifera* seeds during incubation at 20 °C using five replicates of 30 seeds. The bar represents LSD test at $p \le 0.05$



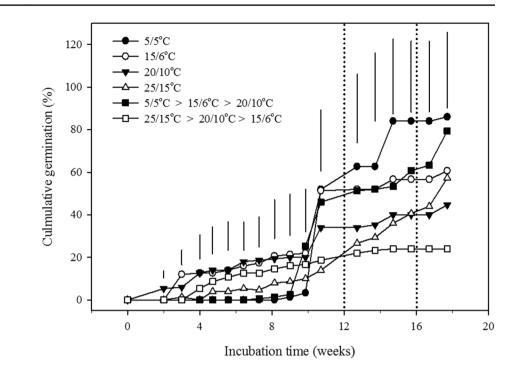
Incubation time (weeks)

Fig. 3 Cumulative germination of *Oenanthe stolonifera* seeds at 5, 10, 15, 20, or 25 °C using two replicates of 100 seeds. LSD bars are present on a given time where statistically significant differences were observed among different temperatures ($p \le 0.05$). No LSD bar indicates no significant differences on that time

germination percentage was about 40% at 15–20 °C, 20% at 10 °C and 25 °C by 11 weeks. The germination percentage of seeds incubated at 5 °C increased from 10% to 36% after 11 weeks.

At 5/5 °C, few seeds (<3%) germinated at 10 weeks, but 86% of seeds germinated at 18 weeks (Fig. 4). A similar pattern of germination was observed at 15/6 °C, reaching

60% after 10-11 weeks of incubation. At 15/6 °C, germination percentage was approximately 22% at 10 weeks and increased to over 50% after 11 weeks. The seeds at 20/10 °C germinated approximately 45% at 18 weeks. Fifty-seven percent of seeds germinated at 25/15 °C after 17 weeks. Germination percentage increased from 3% by 46% between 9 and 10 weeks and reached about 79% at Fig. 4 Cumulative germination of *Oenanthe stolonifera* seeds at 5/5, 15/6, 20/10, 25/15, or a temperature sequence beginning at 5/5 °C or 25/15 °C using three replicates of 50 seeds. LSD bars are present on a given time where statistically significant differences were observed among different temperatures ($p \le 0.05$). No LSD bar indicates no significant differences on that time



18 weeks for seeds under temperature sequence 1 treatment. However, it was about 24% at 18 weeks for seeds under temperature sequence 2 treatment.

The results of embryo growth showed fluctuations at both 5/5 and 25/15 °C (Fig. 5). However, the embryo seemed to elongate after about 6 weeks at both temperatures. The pattern of embryo length at 5/5 °C was similar to that at 25/15 °C. However, the seeds at 25/15 °C began to germinate earlier than those at 5/5 °C (Fig. 5). After 12 weeks, germination percentage was approximately 27.5% or 9.9% at 25/15 or 5/5 °C, respectively.

3.3 Effects of GA₃ treatment on seed germination

Seeds incubated at 5/5 °C did not germinate under all GA₃ treatments. GA₃ had no significant effects on the germination of seeds at 5/5 °C after 30 d of incubation (Table 1). However, seeds at 25/15 °C showed slightly higher germination percentages with increasing GA₃ concentration. The

Fig. 5 Embryo length and cumulative germination of *Oenanthe stolonifera* seeds at 5/5 or 25/15°C (12/12 h) for 11 weeks using five replicates of 50 seeds. The star symbol indicates a significant difference between treatments as determined by Student's *t* test: * $p \le 0.05$; ** $p \le 0.01$; *** $p \le 0.001$

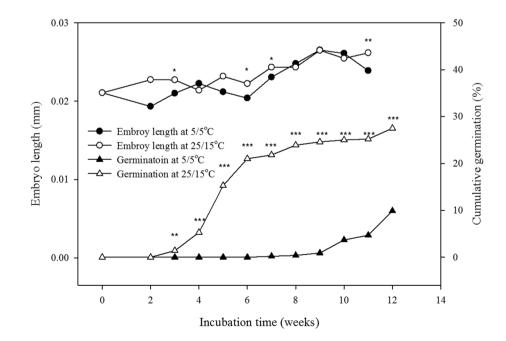


Table 1 Final germination percentage of *Oenanthe stolonifera* seeds treated with 0, 10, 100, 300, or 500 ppm GA₃ at 5/5 or 25/15 °C (12/12 h) for 30 d

$\overline{\text{GA}_3 \text{ concentra-}}$ tion (mg·L ⁻¹)	Temperature (°C)	
	5/5	25/15
0	0.0	0.0 b ^z
10	0.0	0.8 b
100	0.0	2.4 b
300	0.0	3.6 b
500	0.0	11.2 a
Significance	NS	***

^ZAverage values in a column with a different letter are significantly different ($p \le 0.05$) usingTukey's studentized range test (n = 5). NS, *** Non-significant or $p \le 0.001$, respectively

final germination percentage at 25/15 °C was 0, 0.8, 2.4, 3.6, and 11.2% in 0, 10, 100, 300, and 500 mg L^{-1} GA₃, respectively.

4 Discussion

The ribs of Apiaceae fruits can vary in shape and are often suitable for certain forms of dispersal (Cappers and Bekker 2013). The floating capacity of the seed is regulated by the presence of air tissue in the pericarp. *Oenanthe* species occur in ditches and flooded areas. *O. stolonifera* seeds have sponge-like and thickened ribs (Fig. 1), indicating that they rely on water dispersal.

The seed of *O. stolonifera* is a schizocarp with two mericarps unlike an achene of *O. aquatica* (Hroudová et al. 1992). The seed is surrounded by sponge-like and thickened ribs (Fig. 1). It appears to be impermeable. However, the increase in mass once placed in water was 135% after 9 h (Fig. 2). Hence, seeds were able to absorb moisture normally. Therefore, *O. stolonifera* seeds have no PY which is caused by the water-impermeable layers of palisade cells in the seed or fruit coat (Baskin and Baskin 1998, 2004).

According to Hroudová et al. (1992), *O. aquatica* seeds germinated optimally from 20 to 25 °C, and the germination temperature ranged between 5 and 40 °C. At low temperatures, germination of *O. aquatica* seeds was more delayed (Jensch and Poschlod 2008). Similar results have been found in *O. stolonifera* seeds. Kim et al. (1987a) was reported that the optimum temperature for germination was 20–25 °C. In this study, we also confirmed that the seeds germinated better at 20 °C than 5, 10, 15, or 25 °C up until 9 weeks (Fig. 3). However, over 60% of seeds did not germinate until 12 weeks. The remainders of seeds were expected to be dormant due to internal factors.

Seeds of plants belonging to Apiaceae typically have seeds with an underdeveloped embryo at dispersal (Martin 1946). O. stolonifera seeds also have a linear and immature embryo (Fig. 1D). The embryo must grow to a critical length before the radicle emerges. Nikolaeva (1977) defined these seeds as morphologically dormant (MD). MD seeds may germinate within 30 days under favorable conditions (Baskin and Baskin 2004). Kim et al. (1987a) reported that dry seeds germinated only 6-35% at 30 days and cold stratification was needed to increase seed germination, to over 90%. In this study, less than 14% of seeds germinated after 4 weeks at 20, 25, or 25/15 °C (Figs. 3, 4, 5), indicating that these seeds exhibited MD. It is presumed that O. stolonifera seeds partially exhibit MD. A similar result was found in Cicuta virosa, in which seeds had MPD and represented MD about 25% (Cho et al. 2018). In Heloniopsis koreana and H. tubifolra seeds, there was a further increase in germination percentage between 4 and 8 weeks, showing both MD and MPD (Lee et al. 2014). Therefore, we conclude that O. stolonifera seeds primarily exhibit MPD and while some seeds had MD at the time of dispersal.

The seeds with MD have physiological dormancy which is known as MPD (Baskin and Baskin 2004). Seeds with MPD require a considerably longer period of time than those with MD. Eight types of MPD are classified into two categories, simple and complex. In seeds with simple MPD, relatively high temperatures above 15 °C are required to grow embryo, and in those with complex MPD relatively low temperatures between 0 and 10 °C facilitate growth of embryo. In this study, embryo growth in the seeds occurred at both warm and cold temperatures (Fig. 5). Even in seeds with complex MPD, embryo growth can occur at any temperature, but it is the temperature at which embryo growth is complete that determines the temperature required for embryo growth (Fasih and Afshari 2018). Seeds after a period of time germinated to a higher degree at relatively cold temperature regimes than at warm temperature regimes (Fig. 4). Colder temperature for 8-10 weeks may break seed dormancy and increase the germination percentage in O. stolonifera. Thus, O. stolonifera seeds require a period of cold temperatures for embryo growth to be completed. After breaking dormancy and completing the embryo growth, the seeds can germinate within a wide temperature range (even at 5 °C). Thus, we can conclude that the O. stolonifera seeds have the complex category of MPD.

The response of seeds to GA is to determine the three levels of PD: non-deep, intermediate, or deep. The germination of seeds treated with GA could be affected by incubation temperatures (Lee et al. 2014). However, GA does not have the effect of promoting germination as the depth of PD increases (Mamut et al. 2014). In fresh seeds of *O. stolonifera*, GA₃ can promote the germination, even though germination percentage in GA₃-treated seeds was

relatively low at 25/15 °C (Table 1). In seeds with intermediate complex MPD, GA substitutes for cold and moist conditions (Baskin and Baskin 1998). Also, *O. stolonifera* seeds do not show non-deep complex MPD because the seeds germinated over 85% at 5 °C without any warm pretreatments. Therefore, we propose that *O. stolonifera* seeds have intermediate complex MPD.

O. stolonifera is adapted to colonize on emerged river banks and shores of ponds or lakes. Flowers of O. stolonifera occur from late June to early August while fruiting is in July or September, and the aerial vegetative parts are dead and dried during winter. A few seeds of O. stolonifera germinated without any seed pretreatment (Figs. 3, 4, 5). Thus, we presume that those seeds can germinate immediately after dispersal in the natural environment. But the proportion of these spontaneously germinating seeds is not large since most O. stolonifera seeds exhibited MD with physiological dormancy. The embryo in the O. stolonifera seed appear to grow at relatively cold temperatures completely and it has to grow in the seed for 8-10 weeks. Seeds of many wetland species are dormant at maturity and may break dormancy during cold exposure in winter (Baskin et al. 1996). In this study, the germination percentage was promoted by relatively cold temperatures. It is clear that cold temperature is the key factor in breaking seed dormancy. After breaking dormancy, the O. stolonifera seed can germinate even at low temperature, 5 °C. Seeds, which can germinate at relatively low temperatures, can sprout as soon as the temperature starts to rise early in the growing season (Lee et al. 2015). We suggest that O. stolonifera seeds need to avoid unfavorable conditions in winter and form a persistent soil seed bank as a survival strategy.

In conclusion, we propose that *O. stolonifera* seeds possess MPD with MD. In this study, seeds with MD occupied only a small portion, but the portion may be different depending on genetic lines and environmental conditions. GA_3 can break seed dormancy. Cold temperature for 8-10 weeks effectively promoted and increased the germination of *O. stolonifera* seeds under a wide temperature regime. Understanding the requirement for breaking dormancy is crucial to plant management. These results provide useful information for both seed propagation and a practical production plan for *O. stolonifera*.

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Author contributions Kim HJ designed the experiment, analyzed the data, and wrote the manuscript. Na H performed the experiment, analyzed the data, and revised the manuscript.

Compliance with ethical standards

Conflict of interest The authors declare no conflict of interest.

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