Seed Science Research (2004) **14**, 371–378 DOI: 10.1079/SSR2004182

Ecophysiology of deep simple epicotyl morphophysiological dormancy in seeds of *Gagea lutea* (*Liliaceae*)

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Abstract

The effects of temperature on embryo growth, radicle emergence and cotyledon emergence of *Gagea lutea* (*Liliaceae*), a perennial herb widely distributed in Europe, eastern Siberia, the Kurile Islands, Sakhalin and the Far East, were monitored outdoors and in laboratory tests. In Japan, this species inhabits open secondary grasslands and deciduous forests. Seeds with an underdeveloped embryo are dispersed in late May/early June in Hokkaido. The embryo elongates in autumn, and the radicle emerges from the seed in mid-October to mid-November, at temperatures of about 15/4°C. However, cotyledons do not emerge until April, after seeds with an emerged radicle are covered with snow (near 0°C) for about 4 months. In laboratory experiments, temperatures of 25/15°C or 20/10°C followed by 5–10°C were required for embryo growth and radicle emergence. Rate and percentage of cotyledon emergence were promoted by keeping seeds with an emerged radicle under snow. The optimum temperature for cotyledon emergence after 81 d under snow was 15/5°C. Thus, *G. lutea* has deep simple epicotyl morphophysiological dormancy, and this is the first report of epicotyl dormancy in the genus.

Keywords: deep simple epicotyl morphophysiological dormancy, embryo growth, *Gagea lutea*, seed germination, temperature, underdeveloped embryo

Introduction

Although a considerable amount of information is available on seed dormancy in species of the broadleaf deciduous forests in eastern North America, not much is known about seed dormancy in this vegetation type in Japan (Baskin and Baskin, 1998). However, recent studies have shown that seeds of *Erythronium japonicum* (Kondo *et al*., 2002) and *Hepatica nobilis* var. *japonica* (Nomizu *et al*., 2004) have underdeveloped embryos and, thus, morphological or morphophysiological dormancy (MPD) (*sensu* Baskin and Baskin, 1998). Seeds of *E. japonicum* (Kondo *et al*., 2002) seem to have deep simple epicotyl MPD, and this also is true for seeds of *H. nobilis* var. *japonica* (Nomizu *et al*., 2004; personal communication). Our overall long-term objective is to fill a gap in knowledge about seed dormancy in Japanese broadleaf deciduous forests and, thus, to accumulate data on a sufficient number of species to make a valid comparison of the kinds of dormancy in this forest type in Japan and North America. The purpose of the present study is to determine the kind of dormancy in seeds of *Gagea lutea* (L.) Ker-Gawl. (*Liliaceae*).

The genus *Gagea* contains approximately 90 species of herbaceous perennials (Satake *et al*., 1982), and two of them are native to Japan: *Gagea japonica* Pascher and *G. lutea*. *Gagea japonica* occurs on Honshu Island, but it is rare. *Gagea lutea* is widely distributed in Europe, East Siberia, the Kurile Islands, Sakhalin, and the Far East. In Japan, *G. lutea* is indigenous to Hokkaido and from central Honshu northward; however, it is rare in western Honshu and in Shikoku (Satake *et al*., 1982). This species inhabits open secondary grasslands and shady deciduous forests (Takahashi and Tani, 1997). The seeds have an elaiosome and are myrmecochorous (Baskin and Baskin, 1998).

Leaves of *G. lutea* expand immediately after snowmelt in Hokkaido, plants flower from late April until early May and seed set is completed by mid-May. Above-ground parts of individuals have died and disappeared by mid-June. Thus, the photosynthesis period of this spring ephemeral lasts only about 2 months. Various aspects of the biology of *G. lutea* have been studied: genotypic differentiation (Peterson and Peterson, 1999), parasitic fungi (Harasawa, 1968), respiratory metabolism under photosynthetic conditions (Zubkova *et al*., 1997), number of flowers and

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seed set for a population in an open sunny and in shady forest floor conditions (Takahashi and Tani, 1997) and function of multiple flowers with reference to blooming order (Nishikawa, 1998). However, to our knowledge, there has been no research on seed dormancy and germination of this species.

Materials and methods

Seed collection

Most seeds used in this study were collected from a population of *G. lutea* plants growing in a semi-natural grassland at Hokkaido University (43°04′N, 141°20′E), Sapporo, Japan, on 31 May 1999. Ripe fruits were collected from plants with yellow leaves and left to dry in the laboratory for 10 d; most fruits dehisced within this time. Seeds were separated from the dried fruits and used in the experiments carried out in 1999. Seeds used to determine the temperature requirements for cotyledon emergence were collected from the same population at Hokkaido University on 5 June 2003 and left to dry in the laboratory for 7 d.

Phenology of embryo growth and of radicle and cotyledon emergence

In outdoors experiments, seeds were placed in fine-mesh polyester bags and buried in 19-cm-diameter pots filled with a 1:1 volume/volume mixture of peat moss and vermiculite (hereafter called soil). The pots were placed in a non-temperature-controlled metal frame-house at Hokkaido University. This structure was covered by shade cloth from 10 June to 7 November 1999 to simulate forest floor temperature and light conditions. Relative illumination in the frame-house covered by shade cloth was 60%. During the remainder of the year, the shade cloth was removed to simulate open deciduous forest canopy. Soil in the pots was kept moist throughout the experiments. Snowfall began in mid-November 1999, and it covered the ground from the end of November 1999 to 6 April 2000. Temperature at the soil surface in the pots was measured every 15 min throughout the experiment using an electric thermograph, and daily maximum, daily minimum, and daily mean temperatures were calculated.

Phenology of embryo growth

On 10 June 1999, 20 fresh seeds were cut into thin sections using a microtome. Embryo length of each seed was measured under a dissecting microscope equipped with a micrometer (initial embryo lengths). On the same day, 100 seeds were placed in each of five fine-mesh polyester bags and buried 1 cm deep in soil in individual pots in the frame-house.

Twenty seeds were removed at random from the bags every 15 d, and embryo length was measured as described above. Radicles of some seeds began to emerge in mid-October, and by the end of October, radicles had emerged from approximately 20% of the seeds. Embryos in these seeds were recorded as fully elongated (= critical embryo length, 2.24 ± 0.07 mm, n = 15), i.e. embryo length just prior to radicle emergence (see Fig. 1, 7 November). All embryo lengths for any given time were calculated as a percentage of this critical embryo length.

Phenology of radicle emergence

On 10 June 1999, 100 seeds were placed in each of three fine-mesh polyester bags and buried 1 cm deep in soil in individual pots. Seeds in the bags were examined for radicle emergence every 15 d from 10 June to 8 October 1999 and every 5 d from 8 October to 12 November. Seeds with an emerged radicle were removed from the bags, which were then reburied. Mean percentage (± SD) of seeds with emerged radicles was calculated.

Phenology of cotyledon emergence

On 10 June 1999, 200 seeds were placed in each of five fine-mesh polyester bags and buried 1 cm deep in soil in individual pots. On 7 November 1999, seeds with a radicle that had emerged since 28 October were transplanted into new pots (100 per pot) at a depth of 1 cm. Three such pots were prepared to evaluate cotyledon emergence. Seedlings were examined every 30 d between 7 November 1999 and 5 April 2000, and every 5 d between 5 April and 15 May 2000. Seedlings with emerged cotyledons were monitored and removed each time from the pots. Mean percentage (± SD) of seeds with emerged cotyledons was calculated.

Effects of constant and alternating temperatures on radicle emergence

On 10 June 1999, four replicates of 50 seeds each were placed in 9-cm-diameter glass Petri dishes on two layers of filter paper moistened with distilled water, and incubated in temperature- and light-controlled incubators with 12-hour daily photoperiods at five constant temperatures (5, 10, 15, 20 and 25°C) or three alternating temperature regimes (15/5, 20/10 and 25/15°C), where seeds were incubated at the higher temperature for 12 h in light and for 12 h in darkness each day. The light source was 40 W white fluorescent tubes, and photon irradiance at seed level was approximately 20 µmol m^{-2} s^{-1}. Observations were made at 5-day intervals, at which time seeds with an emerged radicle were counted and removed from the dishes. The mean percentage (± SD) of seeds with an emerged radicle was calculated.

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Effects of a high-temperature regime followed by low temperatures on radicle emergence

On 10 June 1999 seeds were placed at 25/15°C for 90 d and then transferred to 5, 10, 15, 20, 25, 15/5, 20/10 or 25/15°C. Seeds were observed at 5-day intervals for radicle emergence at 25/15°C and after transfer from 25/15°C to the second temperature. The starting date of the experiment, number of seeds, method of sowing, light conditions and observations were the same as those described under 'Effects of constant and alternating temperatures on radicle emergence'.

Effects of various temperature regimes followed by 10°C on radicle emergence

Seeds were placed first at temperatures of 20, 25, 20/10 or 25/15°C for 90 d and then at 10°C. The starting date of the experiment and other details are the same as those described under 'Effects of constant and alternating temperatures on radicle emergence'.

Effects of a high-temperature regime followed by 10°C on radicle emergence

Seeds were incubated at 25/15°C for 0 d, 10 d, 30 d, 60 d, 90 d or 120 d and then transferred to 10°C. The starting date of the experiment and other details are the same as those described under 'Effects of constant and alternating temperatures on radicle emergence'.

Effects of temperature on embryo growth

Seeds were maintained at 5, 10 or 25/15°C throughout the experiment, or at 25/15°C for 90 d and then transferred to 5 or 10°C for the remainder of the experiment. Length of embryos in 20 seeds was measured every 10 d, as described under 'Phenology of embryo growth'. Radicle emergence occurred in some seeds throughout the experiment, except at 25/15°C, and the length of the embryo in seeds with an emerged radicle was recorded as that of the critical embryo length. (see Fig. 1, 7 November). The starting date of the experiment and other details are the same as those described under 'Effects of constant and alternating temperatures on radicle emergence'.

Effects of time at 0°C on cotyledon emergence

Seeds were placed into a fine-mesh polyester bag, and the bag was buried in soil in a seed tray (42 × 26 × 8 cm) on 12 June 2003. The tray was placed in the frame-house. Seeds were taken from the bag on 19 November 2003, and 30 seeds with an emerged radicle were buried at a depth of 1 cm in polyethylene containers (80 × 80 × 50 mm) filled with soil. The containers were placed in the frame-house. On 19 November and 21 December 2003, and on 14 January 2004, four containers each were transferred from the frame-house to an incubator at 10°C. On 24 February 2004, four containers each were transferred to incubators at 5, 10, 15, 20 and 15/5°C.

From 5 December to 14 December 2003, temperature at the surface of these containers ranged from –5°C to 5°C. Containers in the frame-house were covered with snow from 15 December 2003 to 2 April 2004, and soil temperature was near 0°C. Therefore, seeds transferred to the incubators on 19 November and 21 December 2003 and on 14 January and 24 February 2004 were exposed to temperatures of about 0°C for 0 d, 16 d, 40 d and 81 d, respectively.

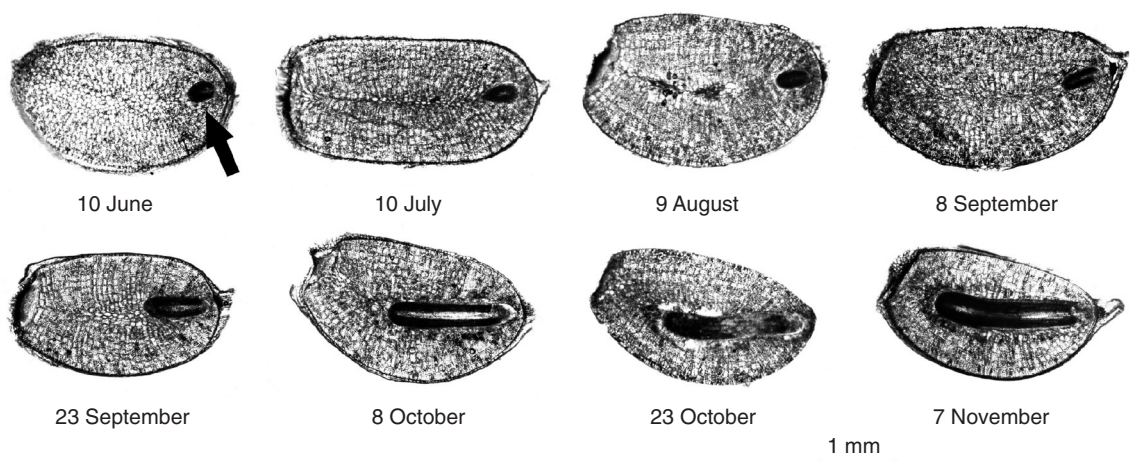

Figure 1. Embryo (arrow) growth in seeds of *Gagea lutea* in a frame-house in Hokkaido, Japan.

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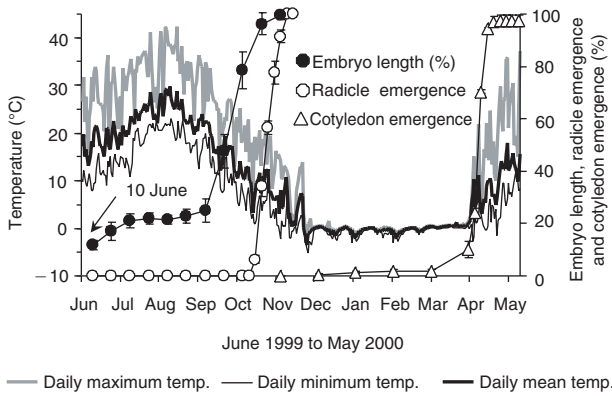

Figure 2. Phenology of embryo growth, radicle emergence (% ± SD) and cotyledon emergence (% ± SD) in seeds of *Gagea lutea* in a frame-house in Hokkaido, Japan. Embryo length (± SD) is expressed as a percentage of the critical embryo length required for germination (see text). Daily maximum, daily minimum and daily mean temperatures were recorded at the soil surface.

Results

Phenology of embryo growth and of radicle and cotyledon emergence

Phenology of embryo growth

Mean (± SD) embryo length in fresh seeds on 10 June 1999 was only 0.27 ± 0.04 mm, which was 12% of critical embryo length. Embryos in seeds buried in pots grew little during the summer (Figs 1 and 2), and mean embryo length on 8 September was 0.56 ± 0.10 mm (25% of critical embryo length); mean daily maximum, mean daily minimum and mean temperatures were 32, 17 and 22°C, respectively, during this period. From 8 September to 7 November, when these temperatures were 20, 8 and 12°C, respectively, embryos grew rapidly. On 7 November, radicles had emerged from 91% of the seeds, and mean embryo length was 2.23 ± 0.04 mm, which was 100% of critical embryo length.

Phenology of radicle emergence

Radicle emergence was first detected on 18 October, and by 12 November a radicle had emerged from 100% of the seeds (Fig. 2). Mean daily maximum, mean daily minimum and mean temperatures from 18 October to 12 November were 15, 4 and 8°C, respectively. Radicle elongation occurred under snow between mid-November 1999 and April 2000.

Phenology of cotyledon emergence

Cotyledons had emerged from only 10% of the seeds by 5 April 2000. Mean daily maximum, mean daily minimum and mean temperatures from 12 November to 5 April were 1, –1 and 0°C, respectively. After snowmelt, cotyledons emerged rapidly from most of the seeds, and final percentage of cotyledon emergence was 97% (Fig. 2). Mean daily maximum, mean daily minimum and mean temperatures for this period (5 April to 25 April) were 12, 2 and 6°C, respectively.

Effects of constant and alternating temperatures on radicle emergence

Seeds at 10 and 15/5°C had the highest rates of radicle emergence (Fig. 3). However, radicles did not emerge in seeds incubated at 20, 25 or 25/15°C, even 180 d after sowing.

Effects of a high-temperature regime followed by low temperatures on radicle emergence

Seeds incubated at 25/15°C for 90 d and then transferred to 20, 25 or 25/15°C did not germinate (Fig. 4). In contrast, seeds transferred to 5, 10 and 15/5°C began to germinate on days 15–20 after transfer, and they had germinated to 99, 100 and 100%, respectively, within 35 d. Radicle emergence of seeds incubated at 20/10°C and 15°C following incubation at 25/15°C for 90 d was delayed, and the germination percentage was low at 15°C.

Effects of various temperature regimes followed by 10°C on radicle emergence

Following 90 d at 20/10, 25/15, 20 or 25°C, radicles emerged from ⩾98% of the seeds 40 d after they were transferred to 10°C (Fig. 5). The hierarchy for rate of radicle emergence at the four temperatures was 20/10 > 25/15 > 20 > 25°C. Radicles emerged from 3% of the seeds during the 90-day treatment at 20/10°C, but 20 d after being transferred to 10°C, they had emerged from 98% of the seeds.

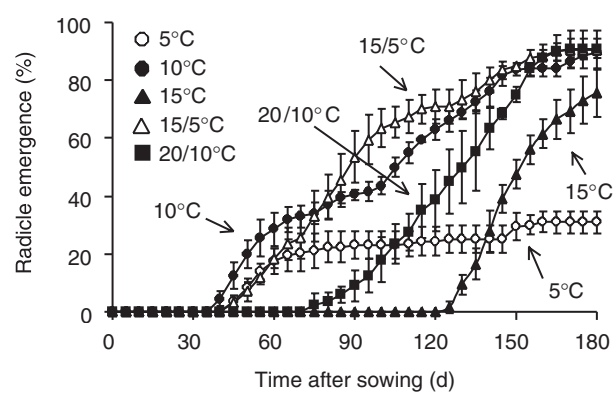

Figure 3. Effects of constant and alternating temperatures on radicle emergence. No radicles emerged from seeds at 20, 25 or 25/15°C. Bars are ± SD.

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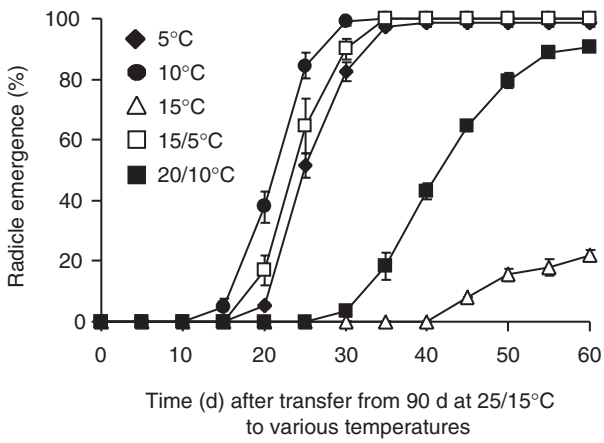

Figure 4. Effects of a 90 d treatment at 25/15°C on radicle emergence in *Gagea lutea* seeds subsequently transferred to various temperatures. No radicle emerged from seeds at 20, 25 or 25/15°C. Bars are ± SD.

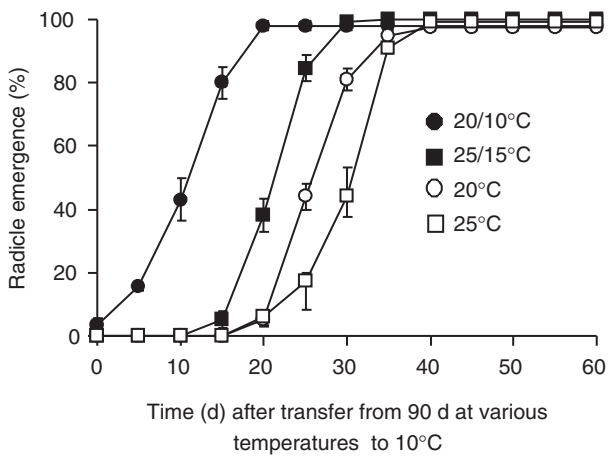

Figure 5. Effects of 90 d pretreatments at 20/10, 25/15, 20 or 25°C on radicle emergence from *Gagea lutea* seeds transferred to 10°C. Bars are ± SD.

Effects of high-temperature regime followed by 10°C on radicle emergence

Radicle emergence was slow for seeds not given an initial treatment at 25/15°C, and only 29% of the seeds had emerged radicles 60 d after sowing at 10°C (Fig. 6). In contrast, the effects of a 25/15°C treatment on radicle emergence were considerable. Radicle emergence for seeds treated at 25/15°C for only 10 d began 30 d after seeds were transferred to 10°C, and the percentage of radicle emergence reached 98% on day 45. Rate of radicle emergence increased with time at 25/15°C. Radicle emergence for seeds treated at 25/15°C for 30 d and 120 d began on days 20 and 11, respectively, after seeds were transferred to 10°C, and final radicle emergence was 100% at 40 d and 30 d, respectively, after seeds were transferred.

Effect of temperature on embryo growth

Embryos of seeds incubated at 5 and at 25/15°C grew little throughout the experiment, and there was no significant difference between the lengths of embryos at these two temperatures. Final lengths of embryos at 5 and at 25/15°C were almost identical: 0.83 ± 0.33 mm (37% of critical embryo length) at 5°C and 0.66 ± 0.11 mm (30% of critical embryo length) at 25/15°C (Fig. 7A). Variation in embryo growth between seeds varied greatly at 5 and 10°C. Only 40% of the seeds had an emerged radicle at 10°C by 120 d, and embryos for which a radicle did not emerge grew to 1.74 ± 0.22 mm (78% of critical embryo length). In contrast, embryos incubated at 25/15°C for 90 d and then at 5 or 10°C grew rapidly after they were transferred (Fig. 7B), and the percentages of seeds from which the radicle had emerged 30 d after transfer were 81% and 92%, respectively. Progress of embryo growth at 5 and at 10°C following incubation at 25/15°C for 90 d was similar to that in the frame-house (Fig. 2).

Effects of time at 0°C on cotyledon emergence

A temperature of 0°C promoted cotyledon emergence, and the percentage of seeds with emerged cotyledons increased with time at 0°C (Fig. 8). Rate of cotyledon emergence was high for seeds (with an emerged radicle) exposed to 0°C for 81 d. The optimum temperatures for cotyledon emergence were 15/5 and 10°C after 81 d at 0°C, and cotyledons emerged from 98% and 80% of the seeds, respectively (Fig. 9).

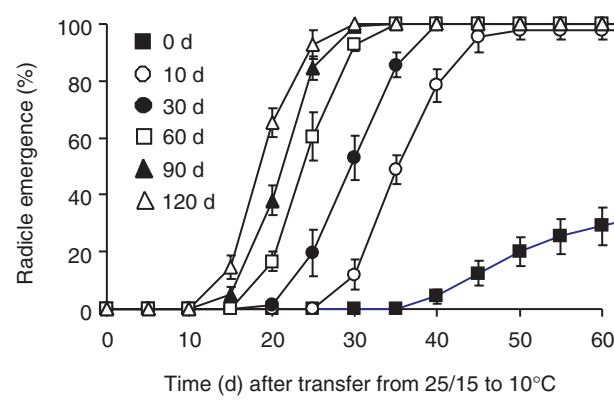

Figure 6. Effects of a pretreatment at 25/15°C for 0 to 120 d on radicle emergence of *Gagea lutea* at 10°C. Bars are ± SD.

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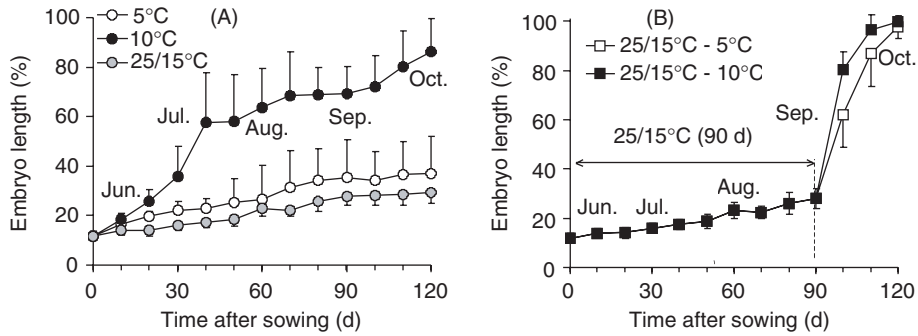

Figure 7. Effects of temperature on embryo growth. Seeds were kept at 5, 10 or 25/15°C throughout the experiment (A) or at 25/15°C for 90 d followed by 5 or 10°C (B). Embryo length (± SD) is expressed as a percentage of the critical embryo length required for germination. Bars are ± SD.

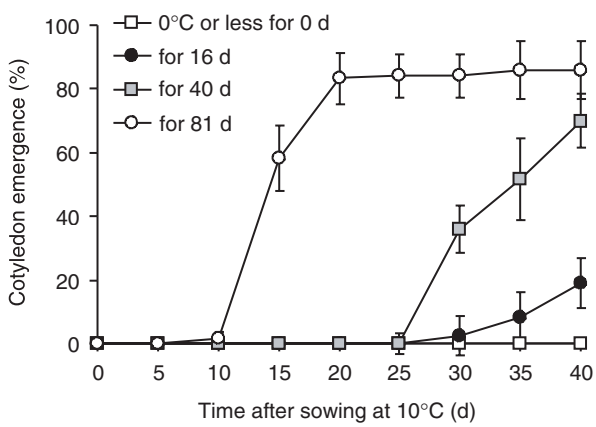

Figure 8. Effects of time at 0°C on cotyledon emergence from seeds with an emerged radicle. Seeds with an emerged radicle were kept outdoors (near 0°C) for 0 d, 16 d, 40 d and 81 d and then transferred to 10°C in an incubator. Bars are ± SD.

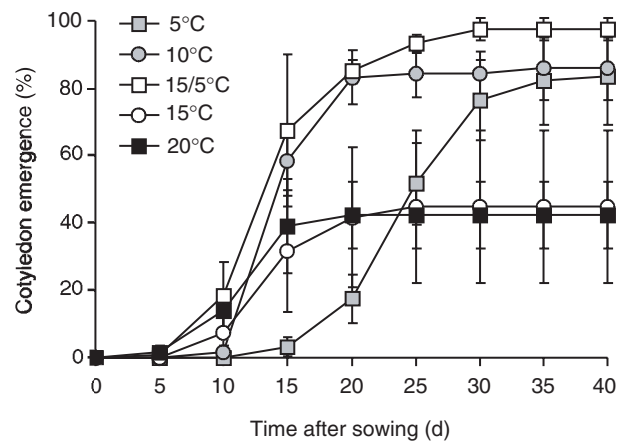

Figure 9. Effects of temperature on cotyledon emergence from seeds with an emerged radicle. Seeds with an emerged radicle were kept outdoors (near 0°C) for 81 d and then transferred to various temperatures in incubators. Bars are ± SD.

Discussion

The phenology of embryo growth, radicle emergence and cotyledon emergence in seeds of *G. lutea* in Hokkaido are summarized in Table 1. Seeds of this species are dispersed in late May, at which time the embryos are underdeveloped (Fig. 1). Embryos grew slowly from early June to early September (Figs 1 and 2), when mean daily maximum, mean daily minimum and mean temperatures were 32, 17 and 22°C, respectively. From early September to early November, when these temperatures were 20, 8 and 12°C, respectively, embryos grew rapidly and uniformly. After embryo growth was completed, radicles emerged uniformly from mid-October to mid-November, by which time 100% of the seeds had produced roots. Mean daily maximum, mean daily minimum and mean temperatures during this period were 15, 4 and 8°C, respectively. Seeds from which a radicle emerged in autumn were exposed to temperatures of around 10°C before snowfall. These temperatures are almost identical to those that occur at the time of cotyledon emergence in early spring. However, cotyledons did not emerge prior to snowfall. In winter, roots elongated under the snow at 0°C. Cotyledons emerged rapidly when mean daily maximum, mean daily minimum and mean temperatures were 12, 2 and 6°C, respectively, in early spring, after approximately 4 months at near 0°C under snow. The requirements for high summer temperatures followed by cool autumn temperatures for embryo growth and radicle emergence, and for low winter temperatures followed by mild spring temperatures for epicotyl emergence, are a phenological adaptation to the seasonal cycle in the temperate region.

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Table 1. Phenology of embryo growth, radicle emergence and cotyledon emergence from seeds in the frame-house in Hokkaido, Japan

Periods	Seed dispersal	Slow embryo growth	Rapid embryo growth	Radicle emergence	Root elongation	Cotyledon emergence
Date	Late May 1999	10 June to 8 September 1999	8 September to 7 November 1999	18 October to 12 November 1999	12 November 1999 to 5 April 2000	5 April to 25 April 2000
Days		90	60	25	145	20
Maximum/minimum temperature (°C)		32/17	20/8	15/4	1/–1	12/2
Mean temperature (°C)		22	12	8	0	6

Results of laboratory experiments on the pattern of embryo growth and radicle emergence were in agreement with observations on these life-cycle events in the non-temperature-controlled metal frame-house. Rapid embryo growth and subsequent radicle emergence required exposure of seeds to temperatures of about 20°C and then placing them at 5–10°C, which were the optimum temperatures for radicle emergence following exposure to high temperatures (Figs 4–7). The mean summer temperature in Hokkaido is approximately 20°C, and autumn temperatures are around 5–10°C when the radicle emerges from *G. lutea* seeds in the field. Even a short period at high temperature had an effect on radicle emergence at 10°C (Fig. 6). Cotyledon emergence from seeds with an emerged radicle was promoted at 0°C, and about 80 d at this temperature was a long enough period for subsequent rapid emergence of cotyledons (Fig. 8). The optimum temperature regime for emergence of cotyledons was 15/5°C (Fig. 9).

The kind of seed dormancy described for *G. lutea* is deep simple epicotyl MPD (epicotyl dormancy) (Baskin and Baskin, 1998). Epicotyl dormancy has been reported in several species in the families *Aristolochiaceae*, *Caprifoliaceae*, *Hydrophyllaceae*, *Liliaceae*, *Paeoniaceae* and *Ranunculaceae* (Baskin and Baskin, 1998). Nikolaeva *et al.* (1985) reported the kind of seed dormancy for seven species of *Gagea*, but not of *G. lutea*. However, none of these seven species of *Gagea* was reported to have epicotyl dormancy. Thus, ours appears to be the first report of epicotyl dormancy for the genus. According to Nikolaeva *et al.* (1985), *G. bulbifera* and *G. taurica* have non-deep simple MPD; *G. pusilla* deep simple MPD; *G. chanae* morphological dormancy (MD); *G. graminifolia* and *G. olgae* non-deep physiological dormancy; and *G. orientalis* physical dormancy (water-impermeable seed coat). It seems possible that *G. graminifolia* and *G. olgae* might have MD or MPD, rather than non-deep physiological dormancy, since physiological dormancy would require that the seeds have a fully developed embryo. Further, it is unlikely that physical dormancy occurs in *G. orientalis*, since the *Liliaceae* is not known to include species with this kind of dormancy (Baskin *et al*., 2000).

The phenology of radicle and cotyledon emergence has been reported for several species with epicotyl dormancy: *Hydrophyllum macrophyllum* (Baskin and Baskin, 1983), *Hydrophyllum appendiculatum* (Baskin and Baskin, 1985a), *Cimicifuga racemosa* and *Hepatica acutiloba* (Baskin and Baskin, 1985b), *Asarum canadense* (Baskin and Baskin, 1986), *Hexastylis heterophylla* (Adams *et al*., 2003) and *Erythronium japonicum* (Kondo *et al*., 2002). The dispersal season for seeds of these species (including *G. lutea*), except *Cimicifuga racemosa*, which is dispersed in autumn (Baskin and Baskin, 1985b), is in May or June. The temperature requirements (season) for root or cotyledon emergence also are basically the same, although there are some differences among the species. Radicle emergence occurs in autumn at low temperatures following a period of high temperatures in summer, and cotyledons emerge in spring after a period of low temperatures during winter.

In Hokkaido, the above-ground parts of *G. lutea*, a spring ephemeral, wither over a period of about 2 months, from early spring to early summer, after the tree canopy closes. Thus, emergence of cotyledons in seedlings with a well-developed root system in early spring means that the plants of *G. lutea* have a long photosynthesis period in high light before canopy closure. Baskin and Baskin (1983, 1985b) suggested that epicotyl dormancy may be adaptive, in that the cotyledons are not exposed to predators and freezing temperatures, and the seedlings have a well-developed root system when the cotyledons expand.

Acknowledgements

This research was supported partially by a Grant-in-Aid for Scientific Research, 11660020, 1999, from the Japanese Ministry of Education, Science, Sports and Culture.

https://doi.org/10.1079/SSR2004182 Published online by Cambridge University Press

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Received 10 May 2004
accepted after revision 23 July 2004