Germination ecology of seeds of the annual weeds *Capsella bursa-pastoris* and *Descurainia sophia* originating from high northern latitudes

C C BASKIN*,†, P MILBERG‡, L ANDERSSON§ & J M BASKIN*

**Department of Biology, University of Kentucky, Lexington, KY, USA, †Department of Agronomy, University of Kentucky, Lexington, KY, USA, ‡Department of Biology-IFM, Linköping University, Linköping, Sweden, and §Department of Ecology and Crop Production Science, Swedish University of Agricultural Sciences, Uppsala, Sweden*

Received 24 February 2003
Revised version accepted 14 October 2003

Summary

Low temperatures may inhibit dormancy break in seeds of winter annuals, therefore it was hypothesized that seeds of *Capsella bursa-pastoris* and *Descurainia sophia* that mature at high latitudes in late summer–early autumn would not germinate until they had been exposed to high summer temperatures. Consequently, germination would be delayed until the second autumn. Most freshly matured seeds of both species collected in August and September in southern Sweden were dormant. After 3 weeks of burial at simulated August (20/10°C) and September (15/6°C) temperatures, 28 and 27%, respectively, of the *C. bursa-pastoris* and 56 and 59%, respectively, of the *D. sophia* seeds germinated in light at 15/6°C. In contrast, in germination phenology studies conducted in Sweden, only a few seeds of either species germinated during the first autumn following dispersal. However, there was a peak of germination of both species the following spring, demonstrating that dormancy was lost during exposure to the low habitat temperatures between late summer and early autumn and spring. Nearly 100% of the seeds of both species subjected to simulated annual seasonal temperature changes were viable after 30.5 months of burial. In the burial study, exhumed seeds of *C. bursa-pastoris* were capable of germinating to 98–100% in light at the simulated spring–autumn temperature regime (15/6°C) in both spring and autumn, while those of *D. sophia* did so only in autumn. In early spring, however, seeds of *D. sophia* germinated to 17–50% at 15/6°C. Thus, most seeds of these two annual weeds that mature in late summer do not germinate in the first autumn, but they may do so the following spring or in some subsequent autumn or spring.

Keywords: dormancy break, germination phenology, germination temperatures, seed germination, winter annuals.

Introduction

An important step in learning how to manage annual weeds is to understand what controls the timing of seed germination under natural conditions. In the case of winter annuals, high summer temperatures promote the full loss of dormancy, while low winter temperatures may wholly or partially, depending on the species, prevent loss of dormancy (Baskin & Baskin, 1986, 1998). Observations in southern Sweden in late August 1997 of large populations of the winter annuals *Capsella bursa-pastoris* (L.) Medic. and *Descurainia sophia* (L.) Webb (Brassicaceae), with the full crop of mature seeds that had not been dispersed, raised several questions. Subsequently, two hypotheses were generated concerning the seed germination ecology of these winter annuals at high latitudes. Firstly, that the seeds are dormant at maturity, and the relatively low temperatures during autumn prevent dormancy loss from occurring; consequently, seeds would not germinate in the first autumn. Secondly, that germination is delayed until the second summer and/or autumn because low temperatures during winter prevent most, or all, of the seeds from coming out of dormancy, i e. dormancy loss would be delayed until late spring and/or summer.

The objective of the research on seeds of *C. bursa-pastoris* and *D. sophia* was to test these two hypotheses. If the first hypothesis is true, seeds would not germinate

Correspondence: Carol C Baskin, Department of Biology, University of Kentucky, Lexington, KY 40506-0225, USA, Fax: 859-257-1717; E-mail: ccbask0@.uky.edu

in autumn of the year in which they are dispersed. If both hypotheses are true, seeds would not germinate until the second autumn. If the first hypothesis is true, but the second is not, seeds would germinate in spring following their dispersal in autumn. A knowledge of the germination ecology of *C. bursa-pastoris* and *D. sophia* seeds that mature in late summer–early autumn in southern Sweden would contribute to our understanding of the ecological life cycles of these species at high latitudes.

Capsella bursa-pastoris occurs in Africa, Asia, Australia, Europe, North America, and South America and *D. sophia* in Asia, Europe, North America, and South America (Holm *et al*., 1979). In the Northern Hemisphere, the range of both species extends to the Arctic Circle or slightly beyond (Hultén, 1962; Best, 1977; Aksoy *et al*., 1998). *Capsella bursa-pastoris* (Runnels & Schaffner, 1931; Chepil, 1946; Roberts & Feast, 1970; Håkansson, 1983) and *D. sophia* (Chepil, 1946; Best, 1977) can behave as facultative winter annuals. With regard to the life cycle of *C. bursa-pastoris* and *D. sophia*, there are two possible reasons why seeds of these two species mature in late summer at high latitudes. First, plants from seeds that germinate in autumn may produce seeds in spring and throughout most of the summer, i.e. not dying after reproduction in spring. Second, plants from spring-germinating seeds do not mature seeds until late summer. Little is known about the differences (if any) in dormancy of seeds produced in late summer by plants resulting from autumn- vs. spring-germinating seeds. Thus, to further test our first hypothesis that seeds which mature in late summer are dormant, seeds of *C. bursa-pastoris* from plants resulting from autumn- and spring-germinating seeds were evaluated for dormancy.

Materials and methods

Seeds of both species were collected in southern Sweden at the locations and on the dates given in Table 1. Latitudes and longitudes for collection sites are: Albacken, 58°20′ N, 15°10′ E; Boxholm, 58°12′ N, 15°02′ E; Vadstena, 58°28′ N, 14°54′ E; and Väversunda, 58°21′ N, 14°42′ E.

In the laboratory, seeds were tested for germination in light (14 h of ≈40 μmol m^{-2} s^{-1}, 400–700 nm, cool white fluorescent light each day) at 12/12 h daily alternating temperature regimes of 15/6, 20/10, and 25/15°C. The light period in each incubator extended from 1 h before the high temperature period began to 1 h after it ended. The temperature regimes simulated mean daily maximum and minimum monthly air temperatures

Table 1 Mean germination percentages of freshly matured *Capsella bursa-pastoris* (SE ranged from 0 to 6%) and *Descurainia sophia* (SE ranged from 0 to 3%) seeds collected in the field in southern Sweden and incubated for 2 weeks in light and in darkness at 15/6, 20/10 and 25/15°C

		% Germination					
		Light			Dark		
Collection date	Collection site	15/6°C	20/10°C	25/15°C	15/6°C	20/10°C	25/15°C
Capsella							
23 August 1997	Boxholm[N]	0	3	7	0	1	0
4 August 1998	Väversunda[N]	3	5	4	1	2	1
4 August 1998	Albacken[N]	3	14	31	3	10	21
4 August 1998	Boxholm[S]	0	5	4	1	4	2
17 August 1998	Boxholm[S]	6	6	4	1	3	3
17 August 1998	Väversunda[N]	5	7	4	1	1	5
17 August 1998	Albacken[N]	2	13	33	3	2	4
17 August 1998	Boxholm[A]	2	7	8	3	2	2
1 September 1998	Albacken[A]	5	4	19	1	2	1
1 September 1998	Väversunda[S]	2	3	4	1	3	4
1 September 1998	Boxholm[S]	1	1	5	1	0	4
15 September 1998	Boxholm[S]	3	5	2	0	1	1
15 September 1998	Väversunda[S]	2	3	3	0	4	1
29 September 1998	Boxholm[S]	2	5	5	0	1	0
29 September 1998	Väversunda[S]	1	4	5	1	1	4
Descurainia							
25 August 1997	Vadstena[N]	4	4	0	1	0	0
4 August 1998	Vadstena[N]	0	0	0	1	0	0
17 August 1998	Vadstena[N]	1	0	1	1	1	0
1 September 1998	Vadstena[N]	0	0	0	1	1	0

[A]Seeds were collected from plants that grew from autumn-germinated seeds.
[N]Not known if the plants (producing the seeds collected for these studies) grew from autumn- or spring-germinated seeds.
[S]Seeds were collected from plants that grew from spring-germinated seeds.

during the growing season in the vicinity of Uppsala, Sweden: May, 15/6°C; June 20/10°C; July, 25/15°C; August, 20/10°C; and September, 15/6°C (Rodskjer & Tuvesson, 1975; Müller, 1982). In some experiments, seeds also were tested for germination in continuous darkness at 15/6, 20/10, and 25/15°C.

Seeds were sown on two sheets of Whatman no. 1 filter paper moistened with distilled water in 55-mm Petri dishes, and unless otherwise stated three dishes with 50 seeds each were placed at each test condition. All dishes were covered with plastic film to reduce loss of water. If seeds were to be tested in darkness, they also were wrapped with two layers of aluminium foil. Germination percentages were determined after 2 weeks, and protrusion of the radicle was the criterion for germination. However, germination usually was completed after 1 week of incubation in light, and at the time germinated seeds were counted most seedlings had fully expanded cotyledons. Each ungerminated seed was pinched with forceps under a dissecting microscope to determine if it contained a firm, white embryo (indicating viability) or a soft, grey embryo (indicating non-viability). Mean germination percentage and SE were calculated for each germination test.

Germination requirements of fresh seeds

The purpose of conducting germination tests on freshly matured seeds was to determine if they were dormant. Ripe seeds were collected on various dates (see Table 1) from plants of *C. bursa-pastoris* growing in three locations (Albacken, Boxholm, and Väversunda) in Östergötland County in southern Sweden and from plants of *D. sophia* in one location (Vadstena) in the same county. Within 2 weeks after each collection, seeds were tested for germination in light and in darkness at 15/6, 20/10, and 25/15°C.

Temperature requirements for dormancy break

On 14 September 1998, ≈1000 seeds of *C. bursa-pastoris* (collected at Boxholm on 1 September 1998) and ≈1000 seeds of *D. sophia* (collected at Vadstena on 1 September 1998) were placed in each of 16 fine-mesh polyester cloth bags for each species. Seeds were stored dry at room temperatures until buried. Each bag was buried in soil (commercial potting mix of mineral soil, humus, peat, and sand) to a depth of 5 cm in 10-cm-diameter pots with drainage holes. For each species, four pots each were placed in an incubator at a constant temperature of 1°C and at the 15/6, 20/10, and 25/15°C alternating temperature regimes. The soil was watered frequently, and the surface of the pots was covered with aluminium foil, thus maintaining moisture levels near field capacity at all times. On the day seeds were buried, other seeds from the same seed lots were tested for germination in light and in darkness at 15/6, 20/10, and 25/15°C.

After 3, 6, 9, and 12 weeks of burial, seeds in one arbitrarily chosen pot each at 1, 15/6, 20/10, and 25/15°C were exhumed and tested for germination in light and in darkness at 15/6, 20/10, and 25/15°C. Three dishes with 50–75 seeds each were placed in darkness at 15/6, 20/10, and 25/15°C, and three dishes with 50 seeds each were placed in light at each temperature regime. To prepare seeds for incubation in darkness, the following procedure was conducted in a completely darkened room: (1) the bag of seeds was removed from a pot of soil, (2) seeds were removed from the bag, (3) a small 'pinch' of 50–75 seeds was sown on moist filter paper in each of the nine dishes, and (4) dishes were wrapped with plastic film and two layers of aluminium foil.

A second investigation of temperature requirements for dormancy break in seeds of *C. bursa-pastoris* was conducted using seeds collected on 17 August 1998 at Boxholm. These seeds were collected from *C. bursa-pastoris* plants that developed from autumn-germinating seeds and from those that developed from spring-germinating seeds (see below). Fresh seeds were tested for germination in light at 15/6, 20/10, and 25/15°C on 29 August 1998. Also, on this date, seeds were buried at 1, 15/6, 20/10, and 25/15°C, as described above, and after 12 weeks of burial they were tested for germination in light at 15/6, 20/10, and 25/15°C. A Mann–Whitney *U*-test (5% level of significance) was used to compare the untransformed means of the number of seeds originating from spring- and autumn-germinated mother plants that germinated after being subjected to the same dormancy-breaking and germination-testing conditions.

The criteria used to distinguish between spring- and autumn-germinated plants were the (i) growth and (ii) development stages of the plants, combined with (iii) their location in relation to timing of soil disturbance. Hence, small plants that were beginning to flower and growing in spring-sown fields were considered to be spring germinated, while large plants that were about finished flowering and occurring in autumn-sown fields were considered to be autumn germinated.

Response of buried seeds to annual seasonal temperature cycle

If buried seeds of *C. bursa-pastoris* and *D. sophia* are subjected to annual seasonal temperature changes, will they be capable of germinating in light at spring temperatures in spring and/or autumn temperatures in

Table 2 Mean germination percentages (SE ranged from 0 to 4%) of *Capsella bursa-pastoris* seeds collected from plants developed from spring-germinated and from autumn-germinated seeds. Seeds were buried for 12 weeks at 1, 15/6, 20/10 and 25/15°C and then incubated for 2 weeks in light at 15/6, 20/10 and 25/15°C

Burial temperature (°C)	% Germination					
	Seeds from spring plants			Seeds from autumn plants		
	15/6°C	20/10°C	25/15°C	15/6°C	20/10°C	25/15°C
Fresh seeds	6	6	4	2	7	8*
1	27	98*	98*	22	52	33
15/6	77*	100	100*	39	97	90
20/10	90	100	100	89	99	99
25/15	98	100	100	97	100	100

*Germination was significantly different ($P \leq 0.05$ by Mann–Whitney *U*-test) in seeds from spring-germinated mother plants than in comparably treated/tested seeds from autumn-germinated mother plants.

Table 3 Mean germination percentages of *Capsella bursa-pastoris* (SE ranged from 0 to 10%) and *Descurainia sophia* (SE ranged from 0 to 2%) seeds incubated for 2 weeks in light at 15/6, 20/10 and 25/15°C following 0–30.5 months of burial in moist soil, during which time seeds were exposed to annual summer-high and winter-low temperatures (see text for temperature regime for each month)

Date seeds were tested	Months of burial	% Germination					
		Capsella			*Descurainia*		
		15/6°C	20/10°C	25/15°C	15/6°C	20/10°C	25 /15°C
15 September 1998	0	1	1	5	0	0	0
1 October 1998	0.5	49	74	78	13	13	0
1 November 1998	1.5	48	99	100	29	16	0
1 April 1999	6.5	89	99	100	17	0	0
1 September 1999	11.5	98	100	100	100	100	0
1 November 1999	13.5	100	100	100	99	55	0
1 April 2000	18.5	100	100	98	49	9	0
1 September 2000	23.5	100	100	100	100	93	1
1 April 2001	30.5	100	100	100	50	28	0

autumn? On 15 September 1998, ≈500 seeds of *C. bursa-pastoris* collected at Boxholm on 1 September 1998 and of *D. sophia* collected at Vadstena on 1 September 1998 were placed in each of six fine-mesh polyester cloth bags for each species and buried in soil in 5-cm-diameter pots, as previously described. Seeds were kept dry at room temperatures until buried. Buried seeds were kept continuously moist and were subjected to an annual summer-high and winter-low temperature regime (June, July, and August, 25/15°C; September and May, 20/10°C; October and April, 15/6°C; November and March, 5/1°C; and December, January, and February, 1°C) until April 2001. At the beginning of the study (15 September 1998), seeds of each species were tested for germination in light at 15/6, 20/10, and 25/15°C. On the dates listed in Table 3, one arbitrarily chosen pot of buried seeds for each species was exhumed and tested in light at 15/6, 20/10, and 25/15°C.

Germination phenology

If sown on the soil surface and subjected to natural seasonal temperature changes, when would seeds of *C. bursa-pastoris* and *D. sophia* germinate? Seeds of *C. bursa-pastoris* were collected from spring- and autumn-germinating mother plants, and seeds of *D. sophia* were collected from mother plants of unknown age (sites and collection dates detailed in Table 4).

All seeds were sown within 1 or 2 days after collection. Three replicates of 200 seeds each were sown on the surface of commercial potting soil in pots (90 mm diameter, 70 mm height) and placed under a table on the north side of a greenhouse, where they were protected from direct rainfall and direct sunlight but exposed to natural temperature conditions in Linköping, Sweden, ≈40–50 km from the collection sites. Temperature was recorded in a parallel pot at 10 mm depth with a Tinytalk-Temp logger (Orion Components Ltd, Chichester, UK). The pots were placed in a tray, and the soil was kept constantly moist by adding water to the tray when needed. The pots were inspected for seedlings weekly or biweekly until 25 November 1999, when the study was terminated.

Results

Germination requirements of seeds collected on various dates

With the exception of seeds collected at Albacken, 92–97% of the seeds of *C. bursa-pastoris* and 96–100% of those of *D. sophia* collected in southern Sweden in

Table 4 Collection sites and times for seeds of (a) *Capsella bursa-pastoris* and (b) *Descurainia sophia* used in studies of germination phenology. Seeds of *C. bursa-pastoris* were from spring- or autumn-germinating mother plants, but time of germination of *D. sophia* mother plants is unknown

	Spring-germinating		Autumn-germinating		
Site	Väversunda	Boxholm	Albacken	Väversunda	Boxholm
(a)					
Collection date (1998)	1 September 15 September 29 September	4 August 17 August 1 September 15 September 1 October	4 August 17 August 1 September	4 August 17 August	4 August 17 August
(b) Germination time of mother plant not known					
Site	Vadstena				
Collection date (1998)	4 August 17 August 1 September				

August and September did not germinate at any temperature regime in light or in darkness (Table 1). Thus, most seeds of these two species were dormant at maturity. Seeds of *C. bursa-pastoris* from Albacken germinated to 3–33% in light and to 3–21% in darkness.

Temperature requirements for dormancy break

In both species, seed viability was near 100% throughout the experiment, and seeds did not germinate during burial regardless of the temperature regime. After seeds were exhumed, little or no germination occurred in darkness. Germination of *C. bursa-pastoris* seeds in darkness ranged from 0 to 11% (with the maximum occurring at 20/10°C for seeds buried at 15/6°C for 12 weeks) and that of *D. sophia* from 0 to 1%. Germination percentages of *C. bursa-pastoris* in light at 15/6, 20/10, and 25/15°C and those of *D. sophia* in light at 15/6 and 20/10°C increased with increase in the temperature at which seeds were buried (Figs 1 and 2). In terms of promoting germination at 15/6°C (simulated spring and autumn temperature) following the shortest period of burial, the optimum temperature regime for breaking seed dormancy in both species was 25/15°C. However, some dormancy break did occur at low temperatures. After 12 weeks of burial at 1°C, seeds of *C. bursa-pastoris* and *D. sophia* germinated to only 30 and 3% in light, respectively, at 15/6°C; however, after 12 weeks of burial at 15/6°C seeds of the two species germinated to 88 and 53%, respectively, at 15/6°C.

In the second investigation of temperature requirements for dormancy break, seeds of *C. bursa-pastoris* originating from spring-germinated mother plants and buried at 1 or 15/6°C germinated to significantly higher percentages than those originating from autumn-germinating mother plants in four of the 12 comparisons (Table 2). Otherwise, differences, if any, between germination of seeds from spring- and of autumn-germinating mother plants were not significant. After 12 weeks of burial at 1°C, seeds from spring- and autumn-germinating mother plants germinated to only 27 and 22%, respectively, in light at 15/6°C; however, after 12 weeks of burial at 15/6°C they germinated to 77 and 39%, respectively, in light at 15/6°C.

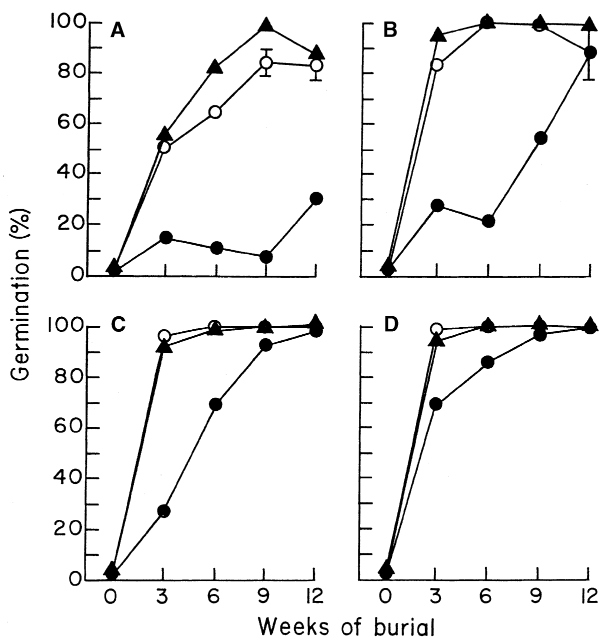

Fig. 1 Germination percentages (mean ± SE, if ≥5%) of *Capsella bursa-pastoris* seeds collected at Boxholm in southern Sweden on 1 September 1998 and incubated in light at 15/6°C (●), 20/10°C (○), and 25/15°C (▲) for 2 weeks following burial at (A) 1°C, (B) 15/6°C, (C) 20/10°C, and (D) 25/15°C.

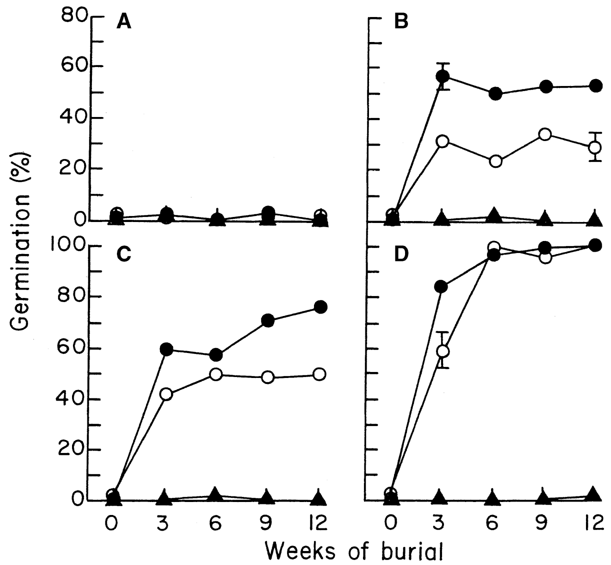

Fig. 2 Germination percentages (mean ± SE, if ≥5%) of *Descurainia sophia* seeds collected at Vadstena in southern Sweden on 1 September 1998 and incubated in light at 15/6°C (●), 20/10°C (○), and 25/15°C (▲) for 2 weeks following burial at (A) 1°C, (B) 15/6°C, (C) 20/10°C, and (D) 25/15°C.

Response of buried seeds to annual seasonal temperature cycle

After 30.5 months of burial, nearly 100% of the *C. bursa-pastoris* and of *D. sophia* seeds were viable, but none germinated during burial. Seeds of both species were dormant when buried in September 1998, but by the following April 89 and 17% of the *C. bursa-pastoris* and *D. sophia* seeds, respectively, germinated in light at 15/6°C (Table 3). However, by September 1999 seeds of both species germinated to 98 or 100% at 15/6°C and 100% at 20/10°C. From November 1999 to April 2001, exhumed seeds of *C. bursa-pastoris* germinated to 100% when tested at the three temperature regimes. However, seeds of *D. sophia* exhibited a seasonal cycle of high germination at 15/6 and 20/10°C in autumn and relatively low germination at these temperature regimes in spring, with germination being higher at 15/6°C than at 20/10°C in spring. Consequently, in the first, second, and third springs following burial many more seeds of *C. bursa-pastoris* than of *D. sophia* (89% vs. 17%; 100 vs. 49%, and 100% vs. 50%) germinated at the spring (15/6°C) temperature regime. In the second and third autumn, however, seeds of both species germinated to near 100% at 15/6°C.

Germination phenology

Regardless of sowing date, only a few seeds of either *C. bursa-pastoris* (Fig. 3) or *D. sophia* (Fig. 4) germinated in the first autumn, but in general germination in the autumn following dispersal decreased with a delay in sowing date. Seeds of *D. sophia* and those from some sowings of *C. bursa-pastoris* began to germinate in late February and early March 1999. However, for all sowing dates of each species, the peak of germination was April. After 10 June 1999, no additional seeds of *D. sophia* germinated, and only 26 seeds of *C. bursa-pastoris* germinated in all pots combined; 20 of them in late June and early July.

Discussion

Seed dormancy combined with low temperatures in the habitat prevent most seeds of *C. bursa-pastoris* and *D. sophia* from germinating during the first autumn following dispersal, i e. the autumn of the year in which they mature. Even seeds of *C. bursa-pastoris* from Albacken, which germinated to a maximum of 33% in light in the 25/15°C incubator when they were first collected (Table 1), germinated to only 3–9% at natural temperatures during autumn (Fig. 3). However, the low germination percentages of seeds from Albacken in autumn is not a surprise because they germinated to only 2–5% in light at 15/6°C (Table 1). Although some dormancy loss occurred when seeds of *C. bursa-pastoris* and *D. sophia* were buried at August (20/10°C) or September (15/6°C) temperatures for 3 weeks (Figs 1 and 2), maximum germination was only 1–16% for *C. bursa-pastoris* and 2–9% for *D. sophia* seeds during the first autumn of the germination phenology study. Thus, lack of high germination percentages in autumn at high latitudes is attributed to decreasing temperatures which inhibit the breaking of seed dormancy, especially for *D. sophia* seeds, and inhibition of germination, especially for *C. bursa-pastoris* seeds. Inhibition of germination at low temperatures, e.g. 1–5°C in November (Fig. 3), would prevent seedlings from appearing late in the growing season when there may not be enough time for them to develop sufficient size and cold hardiness to survive the winter.

The optimum temperature regime for loss of dormancy for both species was 25/15°C, but dormancy break occurred at 15/6°C for some seeds of *D. sophia* and at both 15/6°C and 1°C for many seeds of *C. bursa-pastoris* (Figs 1 and 2). Consequently, some *C. bursa-pastoris* and *D. sophia* seeds subjected to simulated annual seasonal temperature changes germinated in light at 15/6°C the first spring. Also, the germination phenology study showed that some seeds could germinate the first spring. Thus, at high latitudes enough dormancy loss occurs in seeds of both species on relatively mild days in autumn and/or early spring for at least a portion of the seed crop to be capable of germinating in light at spring temperatures in spring. In

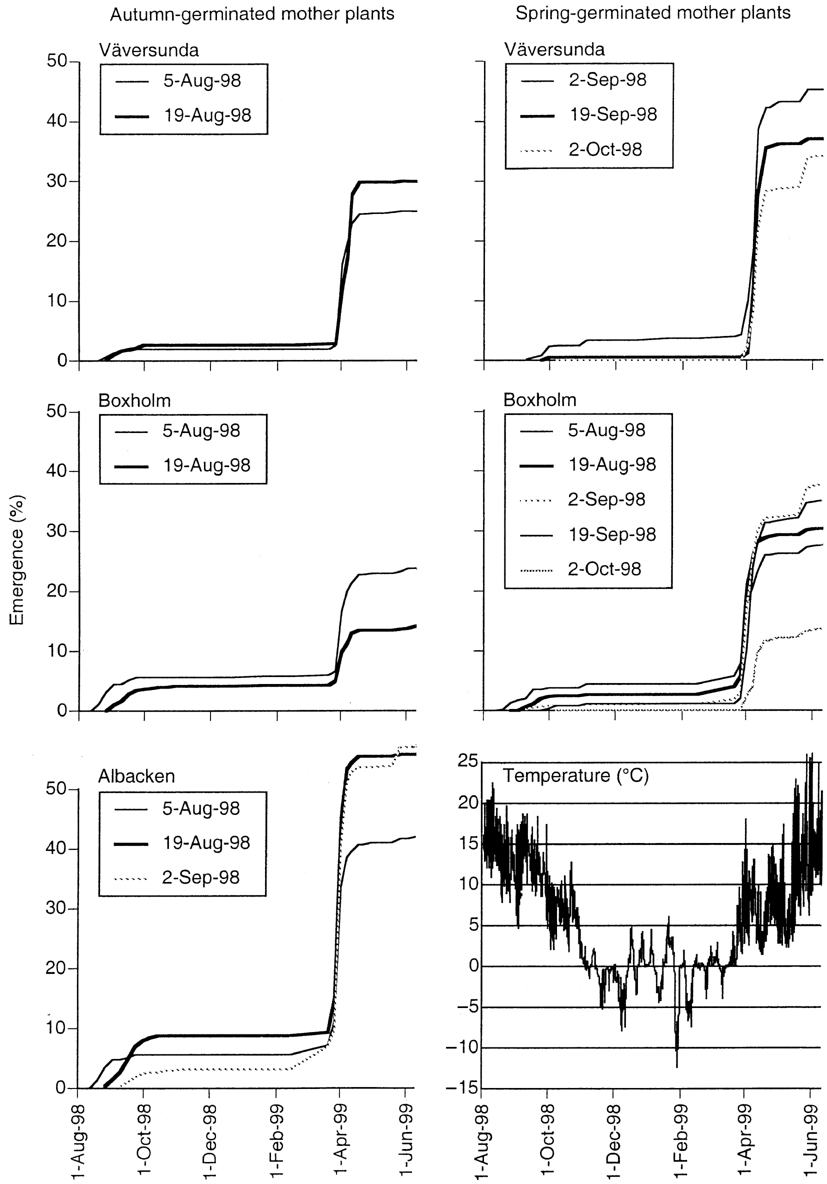

Fig. 3 Germination phenology (from August 1998 to 10 June 1999) of *Capsella bursa-pastoris* seeds collected at Albacken, Boxholm, and Väversunda on various dates in 1998. Data are from three replicates of 200 seeds sown on the soil surface 1–3 days after collection. Temperature was recorded at a depth of 10 mm.

a study of these two species in Uppsala, Sweden, Milberg and Andersson (1997) buried seeds outdoors on 24 November 1994. In March, April, May, and June 1995, maximum germination of exhumed seeds of *C. bursa-pastoris* ranged from ≈12 to 22%, whereas in those of *D. sophia* it ranged from ≈1 to 3%. Thus, more dormancy break occurred in seeds of *C. bursa-pastoris* than in those of *D. sophia* during the low-temperature portion of the year.

The synchronized flush of germination in spring for all sources of seeds of both species suggests the possibility of using a model to predict the timing of *C. bursa-pastoris* and *D. sophia* germination from meteorological data. A predictive model would greatly facilitate weed management by answering questions related to when pre-emergence herbicides should be applied or when mechanical control should be initiated (Forcella, 1998). However, validation of such a predictive model for *C. bursa-pastoris* and *D. sophia* would require repeating the germination phenology study in different years and perhaps in different locations.

In the burial experiment, seeds of *C. bursa-pastoris* remained capable of germinating at 15/6, 20/10, and 25/15°C regardless of how long they were buried. Thus, any seeds of *C. bursa-pastoris* that fail to germinate the first spring probably could germinate at high latitudes at any time during the growing season, if light and soil moisture were nonlimiting. In contrast, at low latitudes in the Northern Hemisphere (e.g. 38°N, 84.5°W, Kentucky, USA) inability of *C. bursa-pastoris* seeds to germinate at high (30/15, 35/20°C) temperatures during summer would prevent them from germinating in June,

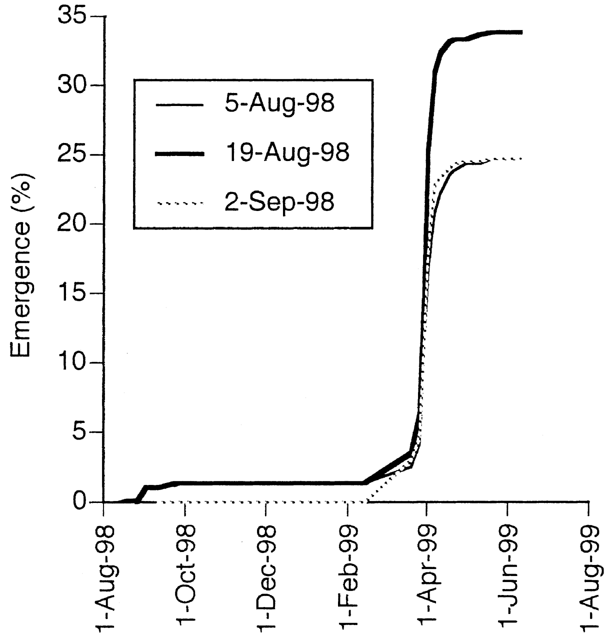

Fig. 4 Germination phenology (from August 1998 to 10 June 1999) of *Descurainia sophia* seeds collected at Vadstena on various dates in 1998. Data are from three replicates of 200 seeds sown on the soil surface 1 day after collection (see Fig. 3 for temperature data).

July, or August (Baskin & Baskin, 1989). However, seeds of *D. sophia* did not gain the ability to germinate at 25/15°C (Fig. 2, Table 3); consequently, germination of this species at high latitudes will probably be restricted to spring or autumn. Moreover, although some seeds of *D. sophia* were capable of germinating in spring, the peak of non-dormancy was autumn. During the 3-year burial study, germination percentage of *D. sophia* seeds exhumed in April and tested in light at 15/6°C was about half of what it had been at the same temperature the previous autumn (Table 3), indicating that low temperatures caused some of the seeds to lose the ability to germinate at 15/6°C. Seeds of *D. sophia* that were dormant in spring underwent dormancy break during summer, and they were capable of germinating to high percentages in light in autumn. In the buried seed experiment conducted by Milberg and Andersson (1997) in southern Sweden, maximum germination of exhumed *C. bursa-pastoris* seeds reached 50% in July 1995, but it did not reach this level in *D. sophia* seeds until September 1995. Thus, it appears that germination of *D. sophia* seeds should peak in autumn, as was observed in Canada by Chepil (1946). However, in the present germination phenology study there was no peak of germination in the autumn of 1999. It is very likely that seeds had become buried over time, e.g. by frost heaving, and their light requirement for germination prevented autumn germination in the absence of soil disturbance.

Significantly more seeds from spring-germinating mother plants of *C. bursa-pastoris* came out of dormancy at 15/6°C and germinated at 15/6°C than those from autumn-germinating mother plants (Table 2). The ecological implication of these data is that compared with seeds from spring-germinating mother plants, germination of more seeds from autumn-germinating mother plants would be delayed until the second autumn after maturation. Consequently, in the first spring after sowing, germination of seeds from spring-germinating mother plants should be greater than that of seeds from autumn-germinating mother plants. This pattern was observed in the germination phenology study for seeds of *C. bursa-pastoris* collected at Väversunda and Boxholm (Fig. 3).

Failure of most seeds of *C. bursa-pastoris* and *D. sophia* to germinate in the autumn of the year in which they were produced means a large reserve of seeds would be present at a site the following growing season. In other studies, some *C. bursa-pastoris* seeds were viable after 5 (Chepil, 1946), 9.7 (Conn & Deck, 1995), 11 (Salzmann, 1954), and 35 years (Telewski & Zeevaart, 2002) of burial, and those of *D. sophia* were viable after 5 (Chepil, 1946) and 9.7 years (Conn & Deck, 1995) of burial. In the present study, nearly 100% of the seeds of both species were alive after 30.5 months of burial at simulated natural temperature regimes, providing additional evidence of the potential of seeds of these species to form persistent soil seedbanks.

Seed production by *C. bursa-pastoris* and *D. sophia* plants in August and September at high latitudes means that few of the freshly matured seeds would germinate if a grain crop was sown at that time. However, numerous seedlings of both species may appear in autumn, especially after soil disturbance, but these would be from seeds produced in a previous year(s). If a crop is sown in spring at a site known to be populated by *C. bursa-pastoris* and/or *D. sophia*, many seeds are likely to germinate, and a high proportion of them may be seeds produced late in the previous growing season. However, some of the seedlings appearing in spring could be from seeds produced in (a) previous year(s).

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