Weed Research, 1989, Volume 29, 205–212

Germination responses of buried seeds of *Capsella bursa-pastoris* exposed to seasonal temperature changes

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Received 20 July 1988
Accepted 17 September 1988

Summary: Résumé: Zusammenfassung

Buried seeds of *Capsella bursa-pastoris* exhibit an annual conditional dormancy/non-dormancy cycle. Seeds after-ripen during summer and remain non-dormant during autumn and winter. Seeds enter conditional dormancy in early spring, first showing marked decreases in ability to germinate at high (35/20°C) and then at lower (30/15, 25/15°C) temperatures. Seeds do not lose the ability to germinate to high percentages at March (15/6°C) and April (20/10°C) temperatures in March and April. Thus, *C. bursa-pastoris* is a facultative winter annual, germinating in both autumn and spring if seeds are exposed to light. However, because some seeds retain the ability to germinate at 30/15 and 25/15°C, they could do so throughout the growing season in regions with cool, moist summers. Conditional dormancy developed in all seeds given 12 weeks at 5°C and subsequently kept for 4 weeks each at March (15/6°C), April (20/10°C) and May (25/15°C) temperatures. Thus, seeds of *C. bursa-pastoris* enter conditional dormancy as temperatures increase in spring.

Variations de la germination de graines enterrées de Capsella bursa-pastoris *exposées à des changements de temperatures saisonniers*

Les graines enfouies de *Capsella bursa-pastoris* suivent un cycle annuel de dormance induite/non dormance. Les graines matures durant l'été demeurent non dormantes pendant l'automne et l'hiver. Les graines entrent en dormance induite au début du printemps, les premiers signes sont une diminution de la faculté germinative à hautes (35/20°C) puis à plus basses (30/15; 25/15°C) températures. Les graines ne perdent pas leur aptitude à germer dans de grands pourcentages aux températures de Mars (15/6) et Avril (20/10°C) en Mars et Avril. Ainsi, *C. bursa-pastoris* est une mauvaise herbe hivernale facultative, germant à la fois en automne et au printemps quand les graines sont exposées à la lumière. Cependant, attendu que certaines graines conservent leur faculté germinative à 30/15 et 25/15°C, elles pourraient se comporter ainsi pendant la saison poussante dans des régions à étés frais et humides. Une dormance induite a été développée par toutes les graines ayant étés placées pendant 12 semaines à 5°C et ensuite exposées à des températures pendant 4 semaines de Mars (15/6), Avril (20/10) ou Mai (25/15°C). Ainsi, les semences de *C. bursa-pastoris* entrent en dormance induite quand les températures augmentent au printemps.

Beeinflussung der Keimung im Boden gelagerter Samen von Capsella bursa-pastoris *durch jahreszeitlich wechselnde Temperaturen*

Im Boden gelagerte Samen von *Capsella bursa-pastoris* unterliegen einem Jahresrhythmus der Dormanz. Während des Sommers reifen die Samen nach und bleiben den Herbst und Winter über nichtdormant. Im frühen Frühjahr tritt eine bedingte Dormanz ein, indem die Keimfähigkeit zunächst bei hohen Temperaturen (35/20°C) und dann bei tieferen (30/15, 25/15°C) deutlich abnimmt. Die Keimfähigkeit bei März- und Apriltemperaturen von 15/6 bzw. 20/10°C geht nicht verloren. So erweist sich *Capsella bursa-pastoris* als eine fakultativ winterannuelle Art, die sowohl im Herbst als auch im Frühjahr keimt, sobald ihre Samen ans Licht gelangen. Da jedoch ein Teil der Samen bei 30/15 und 25/15°C keimfähig bleibt, können diese in Gebieten mit kühlfeuchten Sommern auch in der Vegetationsperiode keimen. Die bedingte Dormanz entwikelte sich in allen Samen, die 12 Wochen lang 5°C ausgesetzt und dann 4 Wochen lang bei März-, April- oder Maitemperaturen von 15/6, 20/10 bzw. 25/15°C gehalten wurden, d.h., daß die bedingte Dormanz der Samen von *Capsella bursa-pastoris* im Frühjahr mit den steigenden Temperaturen eintritt.

Introduction

Capsella bursa-pastoris (L.) Medic. is an annual crucifer native to Europe that has become a cosmopolitan weed of lawns, gardens and waste places (Gleason, 1963). Holm *et al.* (1979) list the species as a serious or principal weed in 15 countries and as a common weed in 17 additional countries. Seeds of *C. bursa-pastoris* have been found in buried seed banks in various countries including Canada (Archibold, 1981), Czechoslovakia (Kropáč, 1966), Denmark (Jensen, 1969; Ødum, 1978), England (Brenchley, 1918; Champness & Morris, 1948; Donelan & Thompson, 1980; Roberts & Chancellor, 1986), France (Barralis & Chadoeuf, 1980), Germany (Hurka & Haase, 1982), Sweden (Zimmergren, 1980), and the United States (Pipal, 1916; Lippert & Hopkins, 1950).

Freshly-matured seeds of *C. bursa-pastoris* are dormant and do not germinate in light or darkness over a range of temperatures (Baskin & Baskin, 1986). Some of the dormant seeds buried in moist soil at 5°C for 12 weeks after-ripened, and when tested in light 40% of them germinated at 15/6 and 20/10°C and 20% at 25/15°C. With an increase in burial temperature, the degree of after-ripening and consequently the maximum temperature for germination increased (Baskin & Baskin, 1986).

Studies on the periodicity of germination of buried viable seeds reveal that those of *C. bursa-pastoris* germinate throughout the growing season, if the soil is disturbed and seeds are exposed to light and adequate moisture (Brenchley & Warington, 1930; Popay & Roberts, 1970; Roberts & Feast, 1970, 1973; Håkansson, 1983; Froud-Williams, Drennan & Chancellor, 1984). These data indicate that buried seeds of *C. bursa-pastoris* either remain non-dormant throughout the year or that they undergo annual conditional dormancy/non-dormancy cycles (*sensu* Baskin & Baskin, 1985). The purpose of our study was to investigate the germination responses of buried seeds of *C. bursa-pastoris* exposed to natural yearly temperature cycles. Also, the responses of non-dormant seeds to simulated winter and spring temperature regimes were determined.

Materials and methods

Seasonal changes in germination responses

Mature, ripe seeds of *C. bursa-pastoris* were collected in Fayette County, Kentucky, U.S.A. (38°N, 84·5°W) on 15 May 1979 and on 25 May 1982. Four days after each collection, about 3000 seeds were placed in each of 27 and 30 fine-mesh (average area of openings 0·13 mm²) nylon bags, respectively. Each bag was buried to a depth of 7 cm in soil in a 15-cm diameter clay pot with drainage holes, and the pots were placed in a non-temperature-controlled glasshouse where the windows were kept open all year. Mean daily maximum and minimum monthly temperatures in the glasshouse for the duration of the study were calculated from continuous thermograph records (Figs 1a & 2a). The soil in the pots was watered to field capacity once each week during summer (1 May–31 August) and each day during the remainder of the year, except on winter days when the soil was frozen. These watering regimes were given to simulate soil moisture conditions that could occur in the field.

Germination tests were done on freshly-matured seeds of each collection. Seeds buried on 19 May 1979 were exhumed and tested on 22 July and 2 September 1979 and on the first day of each month thereafter for 25 months. Seeds buried on 29 May 1982 were exhumed and tested on 1 July 1982 and on the first day of each month until May 1984. Then, 1982 seeds were exhumed and tested on 1 July, 1 September and 1 November 1984 and on 1 March, 1 April, 1 May and 1 June 1985. Germination tests were performed in light- and temperature-controlled incubators at a 14-h daily photoperiod (*c.* 20 μmol m^{-2} s^{-1}, 400–700 nm of cool white fluorescent light) or in constant darkness at alternating temperature regimes (12/12 h) of 15/6, 20/10, 25/15, 30/15 and 35/20°C. These temperature regimes approximate the mean daily maximum and minimum monthly temperatures 2·5 cm below bare soil in northcentral Kentucky during the growing season (Anon., 1968–1973): March, 15/6; April, 20/10; May, 25/15; June, 30/15; July and August, 35/20; September 30/15; October, 20/10 and November 15/6°C. At each temperature regime, the photoperiod extended from 1 h before the high temperature period began to 1 h after it ended.

Seeds were incubated on moist sand in 5·5-cm Petri-dishes. For dark-incubated seeds, three replications of 50–75 seeds each were placed at each temperature regime, and for light-incubated seeds three replications of 50 seeds each were used. All dishes were wrapped with plastic film, and those incubated in darkness also were wrapped with two layers of aluminium foil. All manipulations of dark-incubated seeds were done in complete darkness; thus, these seeds were not exposed to any light between the time they were buried and termination of the germination tests. Final germination percentages were determined after 15 days of incubation, and protrusion of the radicle was the criterion of germination. Standard errors were calculated for all germination percentages.

Response of non-dormant buried seeds to temperature

Ripe seeds were collected in Fayette County, Kentucky, on 27 May 1983 and three days later they were buried in pots of soil and placed in the non-temperature-controlled glasshouse as previously described. The soil was watered to field capacity once each week until 1 September, and then it was watered daily until 1 October. On 1 October 1983, seeds were exhumed and incubated in light at 15/6, 20/10, 25/15, 30/15 and 35/20°C for 15 days. Also, on 1 October 1983, ten pots of seeds were placed at a constant temperature of 5°C in a refrigerator, and two were placed at 30/15°C. The 5°C temperature regime was used to simulate winter temperatures (December–February) because this temperature has been shown to induce non-dormant seeds of winter annuals into dormancy (e.g. Baskin & Baskin, 1984a), and it is near optimal for after-ripening of many seeds that require low temperature stratification to overcome dormancy (Stokes, 1965). After 12 weeks at 5°C, seeds in one pot of soil were exhumed and tested in light over the range of thermoperiods. Six pots of seeds receiving 12 weeks at 5°C were moved to 15/6°C, after 4 weeks at 15/6°C three pots were moved to 20/10°C, and after 4 weeks at 20/10 one pot was moved to 30/15°C. Thus, each time seeds were moved to a higher temperature, controls were left behind. After seeds had been at a new temperature for 4 weeks, they were exhumed and tested in light over the range of thermoperiods, and at this time controls left at preceding temperatures also were exhumed and tested. Seeds placed at 30/15°C on 1 October 1983 were exhumed after 12 and 24 weeks and tested in light over the range of thermoperiods. Soil in all pots of seeds was watered as needed throughout the study to keep it moist. All germination tests were terminated after 15 days. Mean germination percentages and standard errors were calculated.

On 3 June 1984, ripe seeds of *C. bursa-pastoris* were collected in Fayette County, Kentucky, and the study of responses of non-dormant seeds to temperature was repeated. Also, non-dormant seeds were placed at 5°C for 12 weeks and then moved to 30/15°C. After 4, 8 and 12 weeks at 30/15°C, seeds were exhumed and tested in light over the range of thermoperiods.

Results

Seasonal changes in germination responses

Seeds were dormant at the time of burial, and they after-ripened during summer, first becoming conditionally dormant (*sensu* Vegis, 1964) and then non-dormant. They remained non-dormant during autumn and winter and entered conditional dormancy in early spring (Figs 1 & 2). Seeds became non-dormant during the second summer of burial, and the cycle was repeated.

During the five years of the study, the non-dormancy period, with regard to germination in light, was from October to March. During this time, with only a few exceptions, seeds incubated in light germinated to 60–100% at all thermoperiods. In darkness, most of the germination occurred from January to March, and seeds germinated to 9–71% over the range of thermoperiods. Re-entrance into conditional dormancy occurred in March, and it was characterized by marked decreases in germination of seeds incubated in light at 35/20°C in some years and by decreases at 35/20, 30/15 and 25/15°C in other years, and by decreases in darkness at all thermoperiods in all years. In conditional dormancy

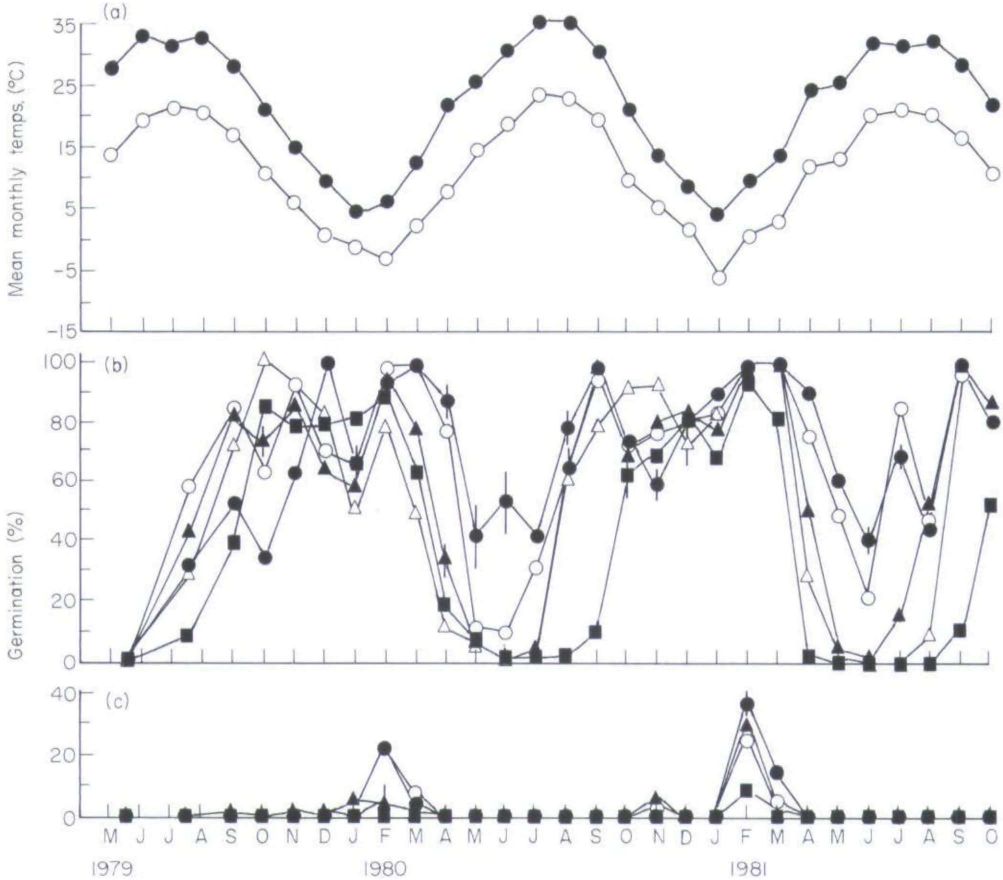

Fig. 1. (a) Mean daily maximum (●) and minimum (○) monthly temperatures in the non-temperature-controlled glasshouse for the duration of the study. (b) Germination percentages (mean ± s.e., if ≥ 5%) of 1979 *Capsella bursa-pastoris* seeds incubated at a 14-h daily photoperiod at 15/6 (●), 20/10 (○), 25/15 (▲), 30/15 (△) and 35/20°C (■) for 15 days following 0–28·5 months of burial in soil. (c) Germination percentages (mean ± s.e., if ≥ 5%) of 1979 *Capsella bursa-pastoris* seeds incubated in continuous darkness at 15/6 (●), 20/10 (○), 25/15 (▲), 30/15 (△) and 35/20°C (■) for 15 days following 0–28·5 months of burial in soil.

seeds germinated in light to 0–42% at 30/15 and 25/15 and to 10–80% at 15/6 and 20/10°C. Germination in darkness decreased to 0–9% at all thermoperiods. As seeds came out of conditional dormancy in summer, they first regained the ability to germinate to high percentages in the light at 15/6 and 20/10°C (if they had lost it) and then at 25/15, 30/15 and 35/20°C. In darkness, germination increased slowly during autumn and winter, reaching a peak in late winter.

Response of non-dormant buried seeds to temperature

Seeds receiving 12 weeks at 5°C germinated to 67 (Table 1) and 24% (Table 2) at 35/20°C, indicating that not all of them had entered conditional dormancy. However, after 24 weeks at 5°C most seeds had entered conditional dormancy, and only 0–15% germinated at 30/15 and 35/20°C. If seeds receiving 12 weeks at 5°C (a time period that simulates winter) were sequentially subjected to simulated March, April and May temperatures, they lost the ability to germinate at 25/15, 30/15 and 35/20°C.

Seeds moved from 5°C directly to 30/15°C entered conditional dormancy after 4 weeks at 30/15°C and germinated to only 13, 14 and 1% at 25/15, 30/15 and 35/20°C, respectively (Table 2). However, these conditionally dormant seeds subsequently after-ripened, and those exhumed after 8 and 12 weeks at 30/15°C showed increases in

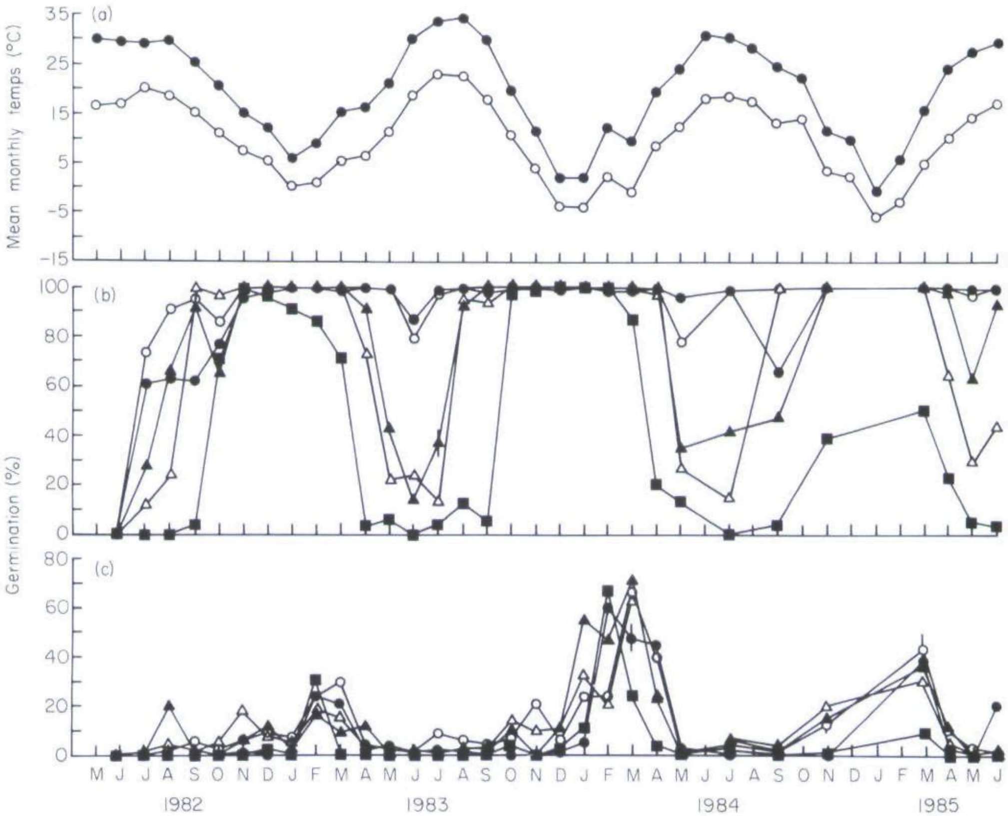

Fig. 2. (a) Mean daily maximum (●) and minimum (○) monthly temperatures in the non-temperature-controlled glasshouse for the duration of the study. (b) Germination percentages (mean ± s.e., if ≥ 5%) of 1982 *Capsella bursa-pastoris* seeds incubated at a 14-h daily photoperiod at 15/6 (●), 20/10 (○), 25/15 (▲), 30/15 (△) and 35/20°C (■) for 15 days following 0–36 months of burial in soil. (c) Germination percentages (mean ± s.e., if ≥ 5%) of 1982 *Capsella bursa-pastoris* seeds incubated in continuous darkness at 15/6 (●), 20/10 (○), 25/15 (▲), 30/15 (△) and 35/20°C (■) for 15 days following 0–36 months of burial in soil.

germination at 25/15 and 30/15°C. Non-dormant seeds kept at 30/15°C for 24 weeks did not enter conditional dormancy.

Discussion

The annual conditional dormancy/non-dormancy cycle exhibited by buried seeds of *C. bursa-pastoris* means that seeds can germinate in autumn and spring, if they are exposed to light. Seeds are non-dormant in autumn, and thus they germinate near to 100% at autumn temperatures. Although seeds enter conditional dormancy in early spring, they do not lose the ability to germinate at March (15/6°C) and April (20/10°C) temperatures during March and April. The ability to germinate in autumn and spring is a characteristic of facultative winter annuals such as *C. bursa-pastoris*. Plants from *C. bursa-pastoris* seeds that germinate in autumn overwinter and flower in spring, and those from seeds that germinate in spring flower in spring and/or summer (Baskin & Baskin, unpublished data; Bosbach, Hurka & Haase, 1982). Sørensen (1954) found a close correlation between the number of leaves and flowering time.

Seeds of *C. bursa-pastoris* sown on soil in a non-temperature-controlled glasshouse in Kentucky germinated in autumn and the following spring, with the peak occurring in autumn (Baskin & Baskin, 1988). In England, Roberts & Feast (1970) obtained germination each month from January through to December with a faint peak occurring in spring, and Popay & Roberts (1970) recorded newly-emerged seedlings from February to September with peaks occurring in February-March, May, June and July, depending on the location of the population. In Sweden, *C. bursa-pastoris* germinated from April through October

Table 1 Germination percentages (mean ± s.e.) of 1983 *Capsella bursa-pastoris* seeds. Buried seeds were allowed to after-ripen in the glasshouse during summer, and then were exposed to various temperature regimes, after which they were exhumed and incubated at a 14-h daily photoperiod at five thermoperiods

	Test thermoperiod (°C)				
Treatment	15/6	20/10	25/15	30/15	35/20
After-ripened seeds	90 ± 1	97 ± 1	91 ± 4	99 ± 1	85 ± 1
Kept at 5°C					
12 weeks	63 ± 1	93 ± 2	95 ± 1	88 ± 4	67 ± 6
16	98 ± 2	100	100	59 ± 5	30 ± 3
20	81 ± 6	91 ± 4	50 ± 5	18 ± 5	5 ± 1
24	77 ± 3	77 ± 2	37 ± 2	7 ± 0	0
5°C (12 w)→15/6°C					
4	100	100	100	55 ± 3	7 ± 2
8	95 ± 2	97 ± 1	63 ± 2	24 ± 6	4 ± 1
12	85 ± 4	89 ± 2	41 ± 4	9 ± 4	1 ± 1
5°C (12 w)→15/6°C (4 w)→20/10°C					
4	88 ± 4	94 ± 1	56 ± 2	26 ± 1	4 ± 1
8	95 ± 3	94 ± 2	49 ± 4	19 ± 2	1 ± 1
5°C (12 w)→15/6°C (4 w)→20/10°C (4 w)→30/15°C					
4	56 ± 2	87 ± 5	8 ± 0	6 ± 1	0
Kept at 30/15°C					
12	89 ± 3	95 ± 3	98 ± 1	99 ± 1	87 ± 4
24	100	100	99 ± 1	100	92 ± 3

Table 2 Germination percentages (mean ± s.e.) of 1984 *Capsella bursa-pastoris* seeds. Buried seeds were allowed to after-ripen in the glasshouse during summer, and then were exposed to various temperature regimes, after which they were exhumed and incubated at a 14-h daily photoperiod at five thermoperiods

	Test thermoperiod (°C)				
Treatment	15/6	20/10	25/15	30/15	35/20
After-ripened seeds	93 ± 1	98 ± 2	100	100	98 ± 2
Kept at 5°C					
12 weeks	91 ± 2	100	100	85 ± 2	24 ± 1
16	90 ± 2	100	96 ± 1	61 ± 5	7 ± 1
20	99 ± 1	100	81 ± 1	22 ± 3	0
24	100	97 ± 2	71 ± 9	15 ± 1	0
5°C (12 w)→15/6°C					
4	77 ± 3	97 ± 2	85 ± 4	43 ± 9	0
8	98 ± 2	100	86 ± 1	32 ± 2	0
12	97 ± 2	99 ± 1	61 ± 4	9 ± 2	0
5°C (12 w)→15/6°C (4 w)→20/10°C					
4	93 ± 3	95 ± 3	73 ± 2	10 ± 3	0
8	98 ± 1	96 ± 2	67 ± 2	15 ± 3	0
5°C (12 w)→15/6°C (4 w)→20/10°C (4 w)→30/15°C					
4	100	100	17 ± 4	3 ± 1	1 ± 1
5°C (12 w)→30/15°C					
4	73 ± 5	100	13 ± 1	14 ± 1	1 ± 1
8	100	99 ± 1	75 ± 5	20 ± 3	1 ± 1
12	99 ± 1	100	94 ± 1	65 ± 8	0
Kept at 30/15°C					
12	97 ± 1	100	100	100	58 ± 6
24	99 ± 1	100	100	100	91 ± 4

with peaks occurring in May and August (Håkansson, 1983). Since buried seeds of *C. bursa-pastoris* do not lose the ability to germinate at 15/6 and 20/10°C, or sometimes not even at 25/15 and 30/15°C, during spring and summer (Fig. 2), seeds brought to the soil surface should germinate at any time during the growing season in regions where summers are relatively cool and moist.

Popay & Roberts (1970) buried seeds of *C. bursa-pastoris* in porous containers outdoors in England, and at 2–4 month intervals for 18 months seeds were exhumed and tested in light at 10 and 20°C. Their study did not reveal that seeds undergo annual conditional dormancy/non-dormancy cycles, because seeds were tested only at temperatures which allow conditionally dormant seeds to germinate. Froud-Williams, Drennan & Chancellor (1984) also buried seeds of *C. bursa-pastoris* outdoors in England, and at 3, 6, 12 and 15 month intervals seeds were exhumed and tested at 20/10°C. Seeds germinated to only about 18–24%, regardless of when they were exhumed.

The implication of germination of seeds of *C. bursa-pastoris* in darkness at spring temperatures in spring is that seed reserves would be slowly depleted by *in situ* germination. However, the germination of exhumed seeds incubated in darkness may overestimate the *in situ* germination of buried seeds in the field. In the present study, germinated seeds were found in the bags of exhumed seeds on only one occasion, March 1980; less than 1% of the seeds had germinated. Also, the maximum germination of seeds buried in nylon bags in the non-temperature-controlled glasshouse in the spring of 1977 and exhumed in November 1977 and at 2-week intervals in March and April of 1978, was only 4% (Baskin & Baskin, unpublished data). Thus, it appears that very few seeds germinate during burial and that some factor(s) of the burial environment, in addition to darkness, may be preventing germination of buried seeds.

Data are limited, but it appears that the time at which seeds of various facultative winter annuals begin to enter conditional dormancy is somewhat correlated with the maximum temperature at which non-dormant seeds germinate to 40% or more. The maximum thermoperiod for 40% or higher germination in non-dormant seeds of *Capsella bursa-pastoris* and *Veronica peregrina* L. (Baskin & Baskin, 1983a) is 35/20°C, and seeds lose the ability to germinate at this thermoperiod in March. In *Lamium amplexicaule* L. (Baskin & Baskin, 1981) and *Veronica arvensis* L. (Baskin & Baskin, 1983b), the maximum thermoperiod of germination is 30/15°C, and seeds lose the ability to germinate at 30/15°C in November and December. In *Aphanes arvensis* L. (Roberts & Neilson, 1982), the maximum thermoperiod for germination is 30/15°C, and seeds lose the ability to germinate at 30/15°C in October and November. In *Veronica hederifolia* L. (Roberts & Lockett, 1978), however, the maximum thermoperiod for germination is 20/10°C, and seeds lose the ability to germinate at this temperature regime in November and December.

The temperature at which non-dormant seeds of *C. bursa-pastoris* enter conditional dormancy differs from that of the facultative winter annuals *Veronica arvensis* (Baskin & Baskin, unpublished data), *Lamium amplexicaule* (Baskin & Baskin, 1984b) and *Aphanes arvensis* (Roberts & Neilson, 1982). Whereas non-dormant seeds of *C. bursa-pastoris* exposed to 5°C for 12 weeks germinated to 24 or 67% at 35/20°C (Tables 1 & 2), seeds of the other winter annuals exposed to 5 (or 4°C for *A. arvensis*) germinated to only 2–21% at 25/15 and 30/15°C (or at 30/10, 30/15 and 30/20°C for *A. arvensis*). The temperature requirements for inducing non-dormant seeds of *Veronica peregrina* into conditional dormancy have not been determined. However, since seeds of *V. peregrina* do not begin to enter conditional dormancy until March, it is suspected that low winter temperatures do not induce them into conditional dormancy.

Seeds of *C. bursa-pastoris* are similar to those of the summer annual *Ambrosia artemisiifolia* L. (Baskin & Baskin, 1980) in that the increasing temperatures of spring induced non-dormant seeds into dormancy. Seeds of *C. bursa-pastoris* enter conditional dormancy, whereas those of *A. artemisiifolia* enter complete dormancy. However, like other winter annuals, seeds of *C. bursa-pastoris* first lose the ability to germinate at high and then at lower temperatures as they enter conditional dormancy. In contrast, *A. artemisiifolia* seeds first lose the ability to germinate at low and then at higher temperatures as they enter dormancy.

Since dormant seeds of *C. bursa-pastoris* exposed to low (5°C) winter temperatures gain the ability to germinate at 15/6, 20/10 and 25/15°C (Baskin & Baskin, 1986), seeds produced late in the growing season potentially could after-ripen during winter and germinate in spring. Thus, seeds produced in the previous springs or autumns could germinate at the same time in spring, if exposed to light.

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