

Germination behaviour in populations of *Capsella bursa-pastoris* (Cruciferae)

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Abstract: Germination behaviour of various *Capsella bursa-pastoris* populations collected from Scandinavia, Middle Europe and the Alps, was tested in unheated, non-illuminated greenhouses (46 populations) and in growth chambers using 5–7 alternating temperature regimes (16 populations). For all populations, the influence of temperature on germination rate is straightforward: the higher the temperature, the greater the germination. Germination capacity, however, may depend on the geographical region. There is also a strong seed age effect on both, rate and capacity of germination. Once dormancy was broken, seeds from all populations were able to germinate over the entire range of temperatures. Some populations revealed a more or less pronounced temperature optimum for germination capacity, others germinated equally well over the entire temperature range. This indicates genetic heterogeneity between populations. However, no correlation between germinability and any environmental pattern was detected. The data indicate that *Capsella bursa-pastoris* has adopted a germination strategy which includes a broad temperature tolerance. Germination of wild *Capsella* plants seems to be regulated by the factors contributing to the inception and breaking of dormancy which depend on pre- and postharvest conditions. Adaptation in germination behaviour in *Capsella bursa-pastoris* is different from that in other life history traits (flowering behaviour, growth form parameters).

In a series of investigations on the adaptation of life history traits of the common and wide-spread weed *Capsella bursa-pastoris* (L.) MED., *Cruciferae*, we have demonstrated that this colonizing species displays definite intraspecific variation in time required for flowering and in several growth form parameters. In addition to a genotypic component, pronounced environmental interactions provide the plants with a strong component of phenotypic plasticity. Correlations to local environmental conditions have been demonstrated (NEUFFER & HURKA 1986 a, b). We have also reported on dispersal mechanisms and the soil seed bank (HURKA & HAASE 1982, BOSBACH & al. 1982). We now report on germination behaviour in natural populations occurring in a wide geographical and ecological range.

Evidence will be presented to demonstrate that *Capsella bursa-pastoris* adopted a germination strategy which includes a broad temperature tolerance. There is no

evidence to the idea for an adaptive genotypic variation pattern. Rather, germination seems to be regulated by dormancy which is strongly influenced by pre- and postharvest conditions.

Material and methods

Along a transect from Northern to Southern Europe seed samples were randomly collected from 20–30 individuals per population. Location maps, geographic co-ordinates and elevations were presented by NEUFFER & HURKA (1986 a, b). We conducted both, greenhouse germination experiments and growth chamber germination experiments. In flower pots 50 seeds per mother plant were separately sown on top of sterile soil (TKS 1 – Einheitserde) and lightly covered with sand grains which would not prevent light penetration. Soil moisture was kept high all the times.

Greenhouse experiments were conducted in unheated, well ventilated glasshouses at the University of Münster (Federal Republic of Germany), without any artificial lighting thus simulating outdoor conditions. Temperature minima and maxima were recorded daily. In subsequent years, different and/or equal (repetitions) seed samples including parental, F₁-, and F₂-generations were germinated.

Growth chamber experiments. Seed samples obtained from individual plants (= families) were divided into subgroups (=subfamilies) and exposed to five (in some cases seven) different temperature regimes. Temperature change followed a 12:12 h interval, synchronously with light and dark, the lower temperature linked to the dark period. Illumination intensity (15000 Lux), air humidity and cultivation conditions were constant for all experiments.

Proportion of seeds completing germination (germination capacity = germinability) was recorded daily. As a measure of the rate of germination we took the number of days, starting from sowing date, required by 50% of the totally germinated seeds to complete germination. It is common to determine the results as percentage of seeds germinated after a certain period of time (final or ultimate germination). In order to fully explore the potential germination behaviour, we set variable arbitrary time limits, particularly with the slowly germinating seeds. A seed was recorded as germinated as soon as the seedling (cotyledones) was visible. Since all seeds were sown on top of the soil it was possible to detect every germinated seed.

Greenhouse experiments

Germination capacity, germination rate and uniformity differed from year to year (Fig. 1). Temperature, seed age and geographical origin may influence the germination behaviour.

Temperature. Yearly variations in germination can partially be explained by fluctuations of temperatures. Highest overall germination percentages in 1978 and 1982 are associated with high daily maxima and minima during the main germination phase. In 1977, an increase in germination capacity of 6% after 38 days when germination seems to be completed, is paralleled by an increase in temperature. Low temperatures in 1976 and in 1980 obviously had a negative influence on germination capacity and germination rate (Fig. 1). Population 281 illustrates the variation in germination capacity between the years (P = parental generation, F₁ = offspring, SA = seed age). 1977: 31% (P, SA: 1, n = 1250); 1978: 79% (P, SA: 2, n = 1250); 1980: 42% (F₁, SA: 2, n = 250).

Seed age. Seed age has a pronounced influence on both germination capacity and rate. When seeds of different ages are sown simultaneously and maintained

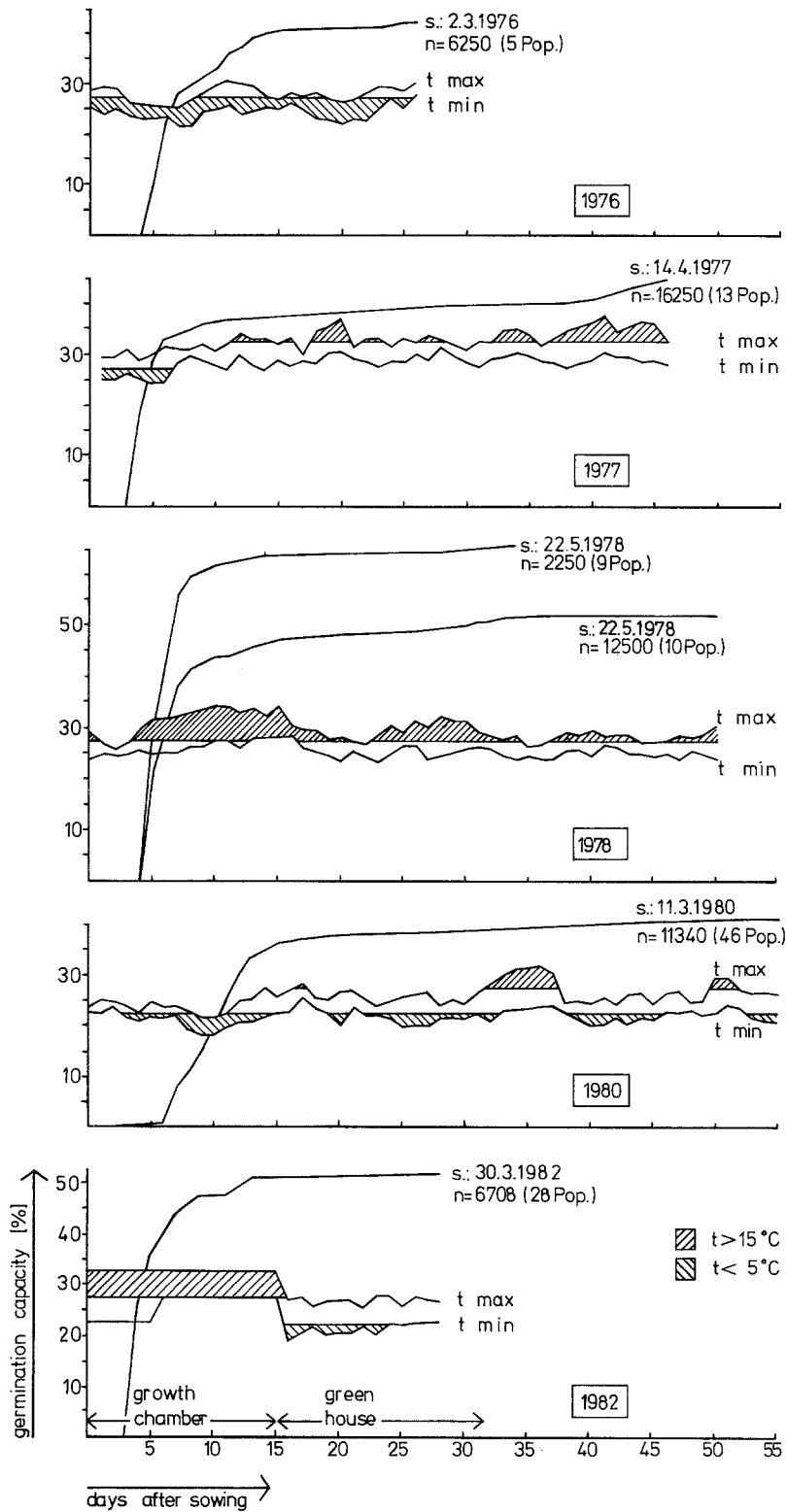


Fig. 1. Germination curves for *Capsella bursa-pastoris* in different years. Daily temperature maxima and minima (t_{\max} and t_{\min}) are given. s Sowing date; n number of seeds

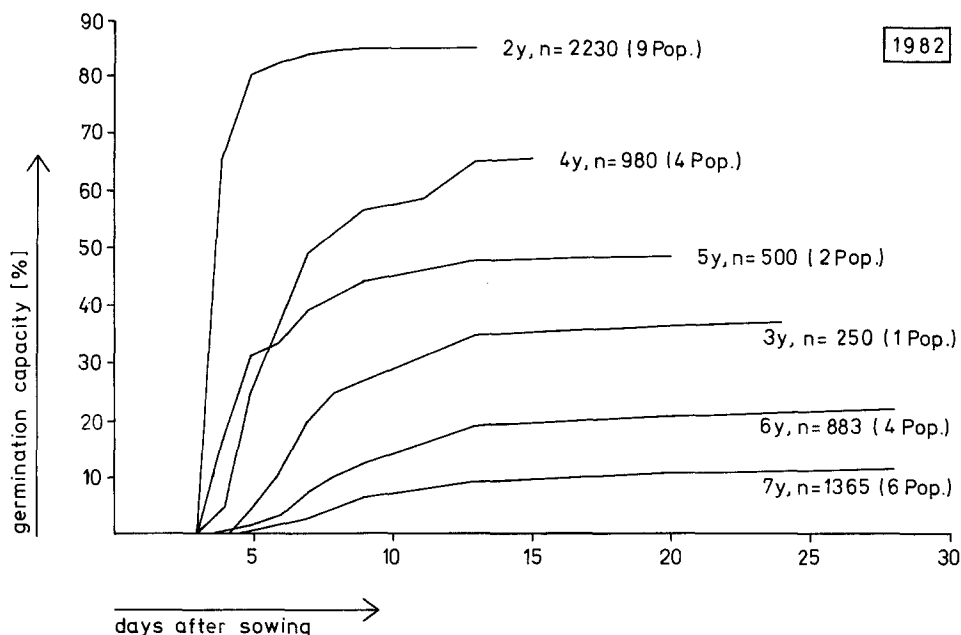


Fig. 2. Dependency of germination capacity and rate of *Capsella bursa-pastoris* on seed age. y Years; n number of seeds

under the same conditions, it appears that the older the seeds the less their germination capacity and the lower their rate (Fig. 2). However, environmental factors, especially temperature, and variation between provenances may strongly interfere with seed age, which is clearly expressed in Table 1. It is obvious from that Table that older seeds may germinate to higher percentage than younger ones (e.g., Pop. 2, 158, 250), whereas equally aged seeds derived from either P- or F₁-generations may germinate with different capacities. The germination capacity of P-generations is higher than that of F₁-generations in Pop. 261 and 280, lower in Pop. 266.

Provenance. Within any given year, pronounced variation between populations in capacity and rate of germination is observed, which cannot be explained by seed age alone (Table 1).

Growth chamber experiments

Table 2 demonstrates that the population samples respond very differently to the temperature treatments. In addition to these interpopulation differences, there are intrapopulation differences, too.

Temperature, general aspects. High temperatures seem to increase germination capacity on a whole. Temperature fluctuations around the daily mean seem to be more important than the mean itself (see data for 5:25 °C and 10:20 °C in Table 2, both with the same daily mean temperature). Relationships between germination capacity and temperature treatments, however, are not straightforward, because they depend on the provenances of the populations. Germination rates, in contrast to germination capacity, are nearly always linked to the same sequence of temperature regimes (Table 3). As one might expect from those findings, the correlation between germination capacity and germination rate is low. However, on an average,

Table 1. Dependency of germination capacity (*GC*) and rate (*GR*) of *Capsella bursa-pastoris* on seed age. Parent generations (*P*) were sown in 1976, 1977 and 1978, all offspring (*F*₁) in 1980. *SA* Seed age in years, *n* number of seeds

Pop. no.	Year	<i>GC</i>		<i>GR</i>		<i>n</i>		<i>SA</i>	
		<i>P</i>	<i>F</i> ₁	<i>P</i>	<i>F</i> ₁	<i>P</i>	<i>F</i> ₁	<i>P</i>	<i>F</i> ₁
2	1976	38	80	5	11	1250	250	2	4
31	1976	33	31	7	11	1250	250	3	4
83	1977	40	13	5	46	1250	250	2	3
90	1977	88	41	4	13	1250	250	2	3
116	1977	26	17	8	46	1250	250	2	3
119	1977	27	21	32	46	1250	250	2	3
147	1977	55	19	5	15	1250	250	2	3
158	1976	37	63	6	8	1250	250	1	4
161	1977	41	30	6	13	1250	250	2	3
172	1977	66	17	4	11	1250	250	2	3
178	1977	67	13	4	22	1250	250	2	3
250	1976	33	74	7	12	1250	210	1	4
253	1976	70	80	7	10	1250	250	1	4
260	1978	33	31	6	13	1250	250	2	2
261	1978	51	12	6	12	1250	250	2	2
264	1978	60	40	7	46	1250	250	2	2
266	1978	50	77	5	7	1250	170	2	2
267	1978	12	26	6	7	1250	250	2	2
276	1977	36	16	42	46	1250	250	1	3
278	1977	50	18	10	46	1250	230	1	3
279	1978	31	24	6	12	1250	250	2	2
280	1978	67	41	7	11	1250	230	2	2
281	1978	79	42	5	6	1250	250	2	2
282	1978	42	32	6	11	1250	250	2	2
294	1977	34	27	4	12	1250	250	1	3

low germination capacity (<25%) corresponds to slow germination rates, higher capacities (>40%) to faster rates.

Seed age. Within all temperature regimes tested, a general decrease of germination capacity with seed age is observed. Rate and uniformity of germination are also affected. The older the seeds the weaker their germination performance (Fig. 3). However, the data indicate that within populations temperatures interfere differently with various seed ages (Table 3): older seeds may show greater germination than younger ones (Pop. 151, 279); germination behaviour of equally aged seeds may significantly vary between temperatures (Pop. 180, 184); seeds of different ages may germinate to the same extent (Pop. 260, 267). With regard to germination rate a similar picture arises but not so distinct because of the straightforward influence of temperature on germination rate.

If dormancy has been terminated, seed age is more likely to influence quantitative aspects of germination than to alter the temperature requirements.

Provenance. Table 2 reveals the capacity and rate of germination within single populations. Sometimes differences between treatment groups within populations

Table 2. Germination capacity (*GC*) and rate (*GR*) of different *Capsella bursa-pastoris* populations under different temperature regimes (in °C). *GR* expressed as the number of days needed to complete 50% germination

Pop. no.	15 : 25		10 : 30		5 : 25		10 : 20		5 : 10		20 : 20		10 : 10	
	GC	GR	GC	GR	GC	GR	GC	GR	GC	GR	GC	GR	GC	GR
83	20	5	30	6	18	15	12	13	11	19				
116	20	3	7	8	28	7	10	17	10	18				
119	20	5	44	5	22	5	15	7	23	29				
147	94	3	84	4	84	5	72	5	90	11	76	3	70	10
151	75	3	75	3	71	4	51	4	65	9	79	3	77	10
180	84	3	69	4	82	5	53	5	43	16				
181	70	3	72	4	83	4	47	5	68	12				
182	81	3	81	4	79	4	75	6	74	12				
184	81	2	90	3	85	4	68	4	73	11				
257 P	19	6	25	7			6	8	8	20				
257 F ₁	64	4	65	4			44	5	71	14				
260	66	3	70	4	86	5	41	6	60	17				
267	58	3	84	5	57	5	67	6	64	19				
276	21	7	23	7	24	10	9	16	2	24				
279	34	5	63	5	59	5	28	7	26	16				
280	59	4	49	5	86	6	39	6	61	17	40	5	18	19
281	84	3	83	4	82	4	65	5	72	11	69	3	40	10
282	52	4	51	5	70	6	36	7	26	16				

Table 3. Temperature preferences for germination capacity (*GC*) and germination rate (*GR*) in different *Capsella bursa-pastoris* populations. Within each population the absolute values for *GC* and *GR* are ranked, 1 standing for the highest value. Equal ranks are not averaged. *SA* Seed age in years

Pop. no.		15 : 25	10 : 30	5 : 25	10 : 20	5 : 10	20 : 20	10 : 10
83	GC	1	1	2	2	2		
	GR	1	2	4	3	5		
	SA	3	5	3	5	6		
116	GC	2	3	1	3	3		
	GR	1	3	2	4	5		
	SA	3	4	3	5	5		
119	GC	2	1	2	2	2		
	GR	1	1	1	2	3		
	SA	3	5	3	5	6		
147	GC	1	2	2	3	2	3	3
	GR	1	2	3	3	5	1	4
	SA	2	1	1	2	2	3	3
151	GC	1	1	1	3	2	1	1
	GR	1	1	2	2	3	1	4
	SA	2	1	1	1	2	3	3

Table 3 (continued)

Pop. no.		15 : 25	10 : 30	5 : 25	10 : 20	5 : 10	20 : 20	10 : 10
180	GC	1	2	1	3	4		
	GR	1	2	3	3	4		
	SA	2	1	1	1	1		
181	GC	2	2	1	3	2		
	GR	1	2	2	3	4		
	SA	2	1	1	1	1		
182	GC	1	1	1	1	1		
	GR	1	2	2	3	4		
	SA	2	1	1	1	1		
184	GC	1	1	1	2	2		
	GR	1	2	3	3	4		
	SA	2	1	1	1	1		
257 P	GC	1	1		2	2		
	GR	1	2		3	4		
	SA	5	5		5	5		
257 F ₁	GC	1	1		2	1		
	GR	1	1		2	3		
	SA	3	3		3	3		
260	GC	2	2	1	4	2		
	GR	1	2	3	4	5		
	SA	2	4	2	4	4		
267	GC	2	1	2	2	2		
	GR	1	2	2	3	4		
	SA	2	4	2	4	5		
276	GC	1	1	1	2	3		
	GR	1	1	2	3	4		
	SA	3	5	3	5	5		
279	GC	3	1	2	3	3		
	GR	1	1	1	2	3		
	SA	2	4	2	4	4		
280	GC	2	3	1	4	2	4	5
	GR	1	2	3	3	4	2	5
	SA	2	3	2	4	4	5	5
281	GC	1	1	1	2	2	2	3
	GR	1	2	2	3	4	1	5
	SA	2	1	1	1	1	3	3
282	GC	2	2	1	3	4		
	GR	1	2	3	4	5		
	SA	2	4	2	4	4		

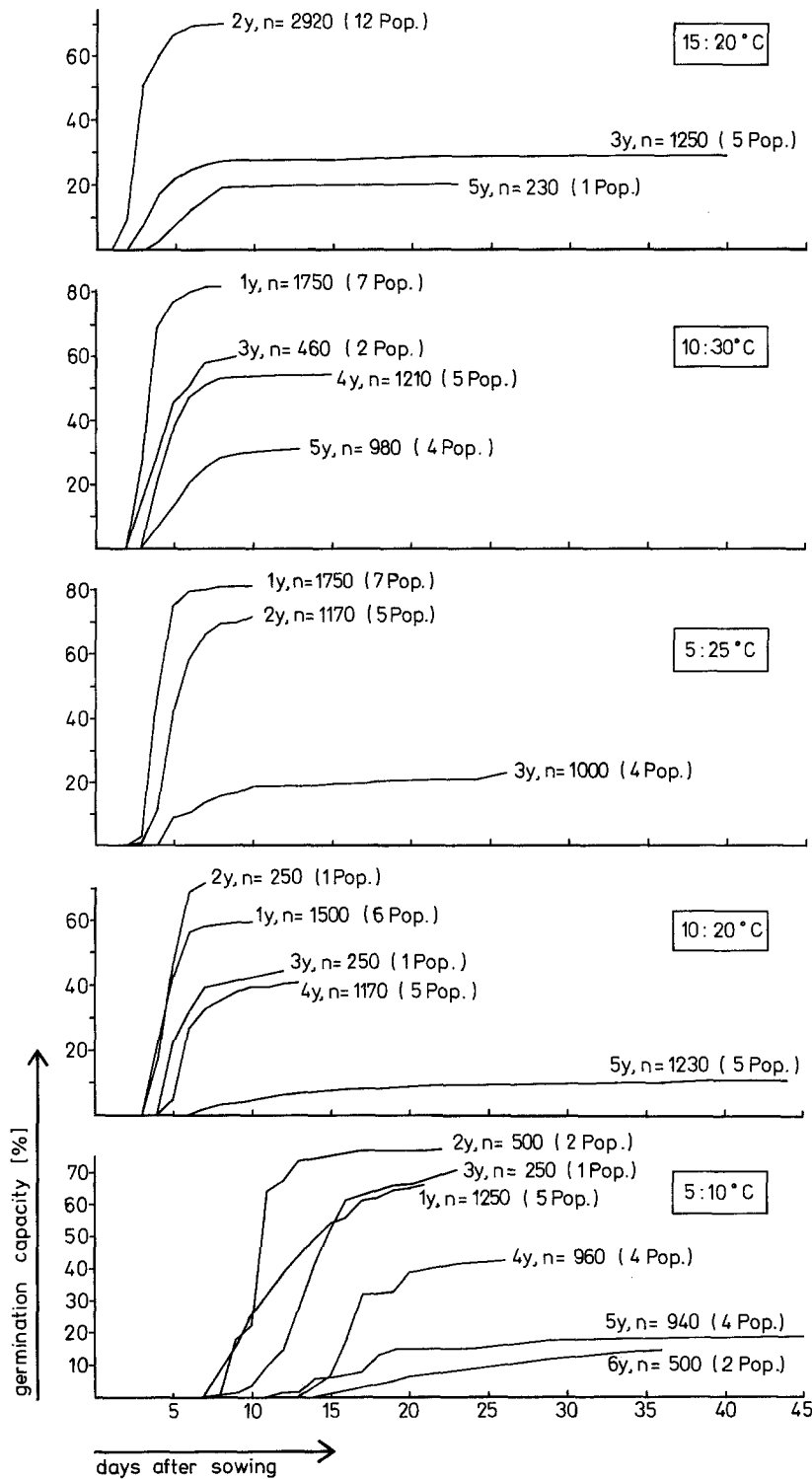


Fig. 3. Capacity and rate of germination of *Capsella bursa-pastoris* under different temperature regimes. Summarized over all experiments within each seed age class. *y* Years; *n* number of seeds

are small; therefore, we conducted a homogeneity test for germination capacity (χ^2 of BRANDT & SNEDECOR, $\alpha = 0.05$). (a) Variability of germination capacity is then generally reduced, but to different extends (Table 3). For instance, Pop. 182 turns out to be completely homogeneous, whereas Pop. 180 still retains considerable variation. (b) Temperature optima for high germination capacity vary considerably between populations other than for germination rate (Tables 2 and 3, cp. Pop. 280 with 281, and 147 with 151). (c) One would expect that at 5:10°C germination behaviour is lowest. However, this is only true for germination rate, not for capacity. The temperature regime 10:20°C equally often yields lowest germination capacity. In those four cases where 10:10 and 20:20 were additionally applied, lowest capacity may include 10:10, even 20:20. (d) We were not able to detect significant evidence for different germination behaviour between Scandinavian and Alpine populations. No correlation between germination behaviour and the altitude of the place of origin of the seed material was detected. The variability between populations is of a similar magnitude, and there is no recognizable temperature preference of any group.

Discussion

A considerable amount of literature on the germination behaviour of *Capsella bursa-pastoris* has been accumulated (MÜLLER 1944, LAUER 1953, ZAIN UL ABIDIN 1956, POPAY & ROBERTS 1970 a, b, ROBERTS & BENJAMIN 1979). However, these investigations did neither provide the necessary data nor do they answer the questions asked within our present research.

Our results indicate that *Capsella bursa-pastoris* shows intraspecific differences regarding the influence of temperature on germination. These differences, however, do not reflect an obvious geographical or seasonal variation pattern. This would suggest that the variation pattern is of a non-adaptive nature. Therefore, we believe that our data indicate a germination strategy adopted by *Capsella* which is characterized by broad temperature tolerances, which is very different from that described by THOMPSON 1973 for *Silene vulgaris*, a species with a similar occurrence over different phytogeographical zones.

Since temperature has been shown to be involved in different aspects of seed germination, especially dormancy, it is essential to us to discuss to what extent seed dormancy is involved rather than germination alone. Second, problems evolve from seed storage effects as is clearly demonstrated in our experiments by the different interference of seed age with germination.

Seed age, longevity, viability. *Capsella* seeds may constitute an important part of the persistent soil seed bank (POPAY & ROBERTS 1970 b, HURKA & HAASE 1982). Long-term burial studies (KIVILAAN & BANDURSKI 1973, TOOLE & BROWN 1946) and seed collections from undisturbed soils (LEWIS 1973) show that *Cruciferae* seeds can be viable after a storage of 30–50 years in the soil (35 years for *Capsella bursa-pastoris* in BEAL's experiment). The loss of seed viability after 4–5 years detected in our experiments seems to be in contrast with these reports. However, it has been demonstrated that air-dried seeds show quicker loss of viability than seeds in the soil. Seed moisture content is a factor closely related to the loss of viability in stored seeds as is storage temperature (see HARRINGTON 1972, 1973). POPAY & ROBERTS (1970 b) report no changes in viability of dried *Capsella* seeds

during a 2-years period, when stored at 4 °C or less. Our seed material was stored at room temperature, hence one might expect a quicker loss of viability. However, as pointed out, there was no strict linear relationship between seed age and loss of germination. This confirms many other observations, that within certain limits a chronometric time scale has little effect on a seed. The limited predictability on seed viability in storage includes genotypic differences, pre- and postharvest conditions, fluctuating storage conditions and effects of oxygen pressure (see BEWLEY & BLACK 1982). All or any one of these factors might attribute to the variation we observed.

Dormancy. *Capsella* displays innate or primary dormancy, secondary or imposed dormancy and relative dormancy (terminology following BEWLEY & BLACK 1985). Primary dormancy in *Capsella* may be terminated by chilling imbibed seeds (POPAY & ROBERTS 1970 a, ROBERTS & BENJAMIN 1979) or by afterripening of dry seeds (ZAIN UL ABIDIN 1956, own experiments). Primary dormancy in *Capsella* is controlled by its seed coat, a treatment with 10% H₂SO₄ increases germination capacity of dormant seeds considerably (ZAIN UL ABIDIN 1956, own experiments). This behaviour is characteristic of almost all light-requiring seeds which have a seed coat imposed dormancy (BEWLEY & BLACK 1985). Secondary dormancy in *Capsella bursa-pastoris* develops in dispersed seeds in response to unfavourable germination conditions. Although secondary dormancy is of great importance in germination ecophysiology, little is known about this phenomenon for *Capsella*. ROBERTS & BENJAMIN 1979 reported that prolonged periods of chilling (more than 14–20 days) resulted in “some” induction of secondary dormancy. Our preliminary results indicate that high temperatures can also induce secondary dormancy. A further complication arises by the fact that *Capsella* seeds do not become non-dormant abruptly, but pass through a period of slow germination rate and/or low capacity. This period is also characterized by an enlargement of its temperature limits until the full potential is gradually reached (relative dormancy).

It is long known that the degree of primary dormancy may be strongly influenced by environmental and physiological factors operating during ripening of the seeds on the mother plant (“maternal effects”). These preharvest factors include temperature effects, photoperiod, light quality, nutrition, maturity at harvest, seed size and seed morphology. The degree of primary dormancy may also be of a genetic nature (for review, see BARTON 1965, STOKES 1965, EVENARI 1965, LANG 1965, BEWLEY & BLACK 1982, 1985).

Induction and emergence from dormancy is probably the most important factor in regulating seedling emergence of *Capsella* in natural conditions. Although this aspect has not been thoroughly studied many signs indicate the great influence of environmental factors on dormancy in *Capsella*. For instance, there seems to be no doubt that the seed material of ZAIN UL ABIDIN (1956), collected in Southern Germany, was less dormant than that of POPAY & ROBERTS 1970 b and of ROBERTS & BENJAMIN 1979 (collected in England). MÜLLER (1944) describes that seeds harvested at different years from the same locality and allowed to afterripen at equal conditions (at least 10 months under dry storage) differed greatly in germination behaviour. SALISBURY (1963) reports intermittent germination of seeds collected from a single mother plant. His research demonstrates the role of the environment in dormancy release, as well as in dormancy inception. HURKA & BENNEWEG (1979) presented information which demonstrates the influence of seed

size on germinability. ZAIN UL ABIDIN (1956) reported that germination capacity of *Capsella* seeds collected in the field exceeded that of seeds raised in the greenhouse by 15%, which agrees with our results. Furthermore, we often observed that seeds obtained from field experiments show greater germination performance than those which were collected at their natural sites. We attribute this partly to maternal effects as harvesting time can be optimally adjusted in the field station.

Light quality and photoperiodic effects have an important role in dormancy inception and breaking (see FRANKLAND & TAYLORSON 1983). In *Capsella*, seeds shaded by a leaf canopy frequently only germinate upon removal of the vegetation cover (POPAY & ROBERTS 1970 b, BOSBACH & al. 1982). This is evidence for indicating the action of the phytochrome system in germination behaviour. CRESSWELL & GRIME (1981) compared seeds of species which mature while the surrounding tissues (fruits or seed coat) remain green, with those whose covering tissues have little chlorophyll at maturity. Those lacking chlorophyll had little or no light requirement for germination, while the chlorophyll bearing – including *Capsella* and other Crucifers – are light-requiring. The explanation they provide is that the light transmitted through the chlorophyll-rich tissue, is rich in the far-red component and thus lowers the amount of P_{fr} . We detected one seed lot of *Capsella bursa-pastoris* collected in the field which rapidly germinated in the dark to the same high level as in light (unpubl. data). Such a performance might be attributed to the light quality received during seed maturation for this seed collection.

Germination strategy of *Capsella*. The effect of temperature on germination alone and the role of temperature in terminating dormancy must be considered separately. However, it is difficult to separate them in practice. Nevertheless, it is essential for the following discussion to consider whether our seed material had emerged from dormancy or not. Based on all that is known about dormancy release in *Capsella* under dry storage conditions, we feel justified to regard our seed material as non-dormant. The low germination rates in some of the seed lots can mostly be attributed to the loss of viability.

All populations were able to germinate over the whole range of temperature regimes, although with different germination peaks. Temperature alters significantly the germination rate but, other than with germination capacity, its influence is the same in all tested samples. The differential preferences to temperature between populations would suggest genetic heterogeneity. However, we could not establish convincing evidence for a correlation between this pattern and any environmental pattern. Our data suggest that germination of *Capsella bursa-pastoris* in the field is mainly regulated by dormancy and by the influence of temperatures on the rate of germination. Since dormancy inception and release is highly influenced by environmental factors, this appears to be a satisfactory way to regulate seedling emergency, in time and space, for *Capsella* which occupies a wide range of soil types, climatic conditions and which has to cope with the unpredictability of its habitats. Such a germination strategy comes close to an “all purpose genotype” as proposed by BAKER (1974).

The flowering behaviour of *Capsella bursa-pastoris* revealed definite intraspecific variation with significant adaptation to climatic conditions (NEUFFER & HURKA 1986 a). Growthform parameters were found also to possess adaptive genotypic differentiation (NEUFFER & HURKA 1986 b). The present study on germination behaviour, however, does not support the idea of adaptive genotypic differentiation.

Capsella bursa-pastoris adopts different strategies associated with several life history traits.

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