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Gen-ecology of *Capsella bursa-pastoris* from an altitudinal transsect in the Alps

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Summary. Seeds were collected in wild populations of *Capsella bursa-pastoris* growing along a cline from low elevations to the high mountain region in Switzerland. Progeny were grown in open field random block experiments and a number of relevant characters was measured. Germination behaviour showed no relationsship to the place of origin and exhibits considerable phenotypic plasticity. Flowering, plant height, rosette diameter and leaf forms displayed genotypic variations that were correlated with altitude. Along the considered altitude gradient phenotypic plasticity was overruled by genetic variation. Later flowering genotypes replaced the earlier flowering genotypes along the topocline which indicates retarded maturity and prolongation of the life cycle at high altitude.

Key words: Ecotype – *Brassicaceae* – Flowering – Germination – Growth form

Common features of weedy plants often include adaptation to a wide range of environments. This can be achieved by considerable phenotypic plasticity, as well as ecotypic differentiation. Marked local differentiation due to founder effects and restricted gene flow as a consequence of predominant self-pollination is another common feature of colonizers (Brown and Marshall 1981).

It has been postulated that genetic variation and phenotypic plasticity may be alternative strategies (Brown and Marshall 1981). Phenotypic plasticity appeared to replace genetic variation in three pairs of congeneric *Avena-*, *Bromus-*, *Limnanthes*-species (see Jain 1979). However, reviewing more recent literature, Quinn 1987 argues that there is "no reason to suspect that selection for genetic variation and phenotypic plasticity would always be naturally exclusive". Extensive studies on *Capsella bursa-pastoris* (L.)Med. (*Brassicaceae*) revealed high degree of genetic and phenotypic variation in life history traits of European populations (Neuffer and Hurka 1986a and b). Genetic adaptations of certain traits to local ecological conditions were evident. Populations also varied in the amount and pattern of plasticity and it appeared that the phenotypic plasticity may be also controlled by selection. In addition to marked geographical differences between Scandinavian and Alpine populations a strong correlation between time of flowering and elevation above sea-level was observed in Alpine populations (Neuffer and Hurka 1986a). In the light of the variation in the genetic system and phenotypic plasticity among these populations, it seemed highly desirable to further analyze this situation in *Capsella*. It will be shown that along an altitudinal gradient from 300 m to 2000 m above sea level *Capsella* evolved over such a short distance of only a few 4 km local distinct populations which followed the environmental cline. This differentiation has a marked genetic component especially for flowering, plant height and leaf form.

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Methods

Along a cline from 300 m to 2000 m in the Alps the Switzerland individual seed samples were randomly collected from natural populations of *Capsella bursa-pastoris* (Fig. 1). Progeny was raised from the seed samples and a number of characters registered: germination, time to flowering, and growth form parameters such as leaf morphology, plant height and rosette diameter.

Fifty seeds per plant were separately sown on top of sterile soil in pots and lightly covered with sand, which

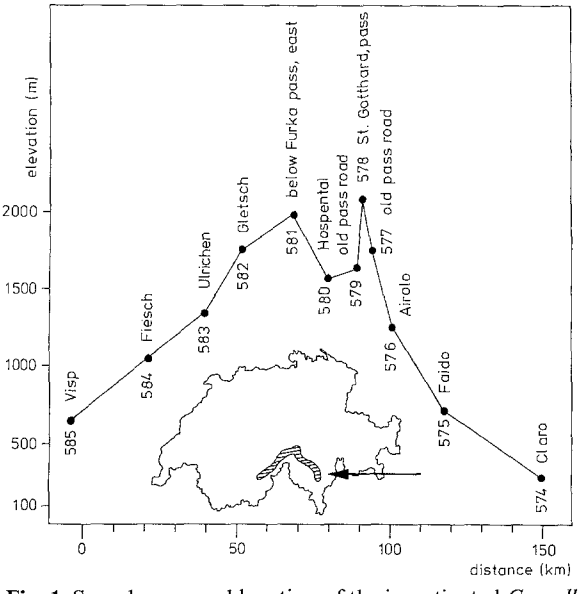

Fig. 1. Sample area and location of the investigated *Capsella* poulations

allowed light penetration. Soil was continually kept moist. This experiment was conducted in unheated, well ventilated glasshouses at the University of Osnabrück (FRG), without artificial lighting to simulate outdoor conditions. Sowing date was March 15, 1984. The proportion of seeds completing germination (germination capacity = germinability) was recorded daily. As a measure of the rate of germination, we used the number of days starting from sowing date that were required for 50% of complete germinated seeds to fully germination (germination rate). A seed was recorded as germinated as soon as the cotyledons became visible.

Open field experiments

Progenies raised from the collected seed samples (7–27 per population) were grown in random block experiments in the field station of the University of Osnabrück (52.18° N, 8.00° E, 70 m above sea-level), FRG. The progeny of a single mother plant (normally 10 individuals) is called a family. Due to unequal germination (dormancy effects) and/or mortality during the experiment family sizes varied. Field data were collected from May 18 to October 30, 1984. The opening of the first flower bud was defined as the beginning of flowering. Rosette diameter and plant height were also recorded. One typical rosette leaf from each plant, usually between the 8th and the 12th to develop within the rosette, was collected and deposited in the Herbarium of the University of Osnabrück. These leaves were classified following Shull 1911.

Statistical evaluation

Correlation and regression analysis were carried out; the assumption of linearity is based on the distribution of the data pairs within the scatter diagram. Unifactoriall analysis of variance (ANOVA) was carried out. Families with less than 5 values were omitted. A non-parametric variance test (*H*-Test of Kruskal and Wallis) was also conducted. To detect homogeneous groups of means within populations, least significant differences (LSD) tests following ANOVA were employed. The meaning of the LSD-groups should be shortly commented. These groups are characterized by similar phenotypes. As the phenotypes can be modified by the environment, number and size of the LSD-groups may change from experiment to experiment and, therefore, should not be taken as quantitatively absolute. However, phenotypic similar groups point the existance of genotypes which under a given environment express similar phenotypes.

Whereas ANOVA provides information whether there are differences between groups (= families) within populations or not, the LSD-groups can provide qualitative estimates of the organisation of the within population variability.

Results

Germination

No obvious relationship between germination capacity and germination rate and the place of origin (e.g. elevation) was detected (see Fig. 2). In many cases, a high germination capacity seemed to be correlated with a high germination rate (Fig. 3). However, we also observed high germination

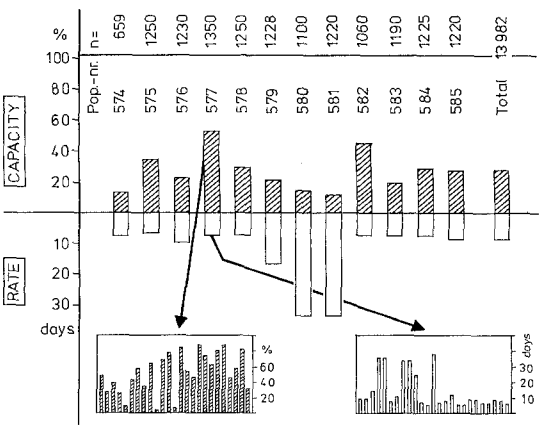

Fig. 2. Germination capacity and germination rate summarized for all families within each populations. Insert: Intrapopulation variability (family values) for pop. 577, left: capacity; right: germination rate

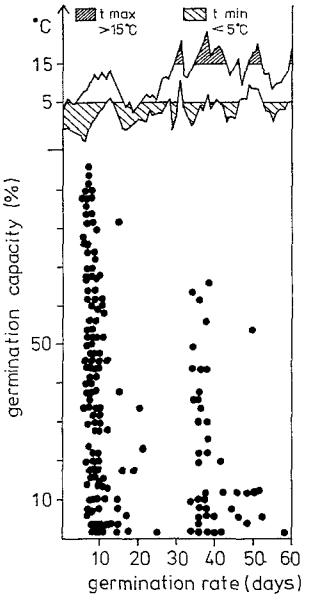

Fig. 3. Germination capacity and germination rate for all families. Daily air temperatures for Osnabrück at the top of the diagram

capacity with slow germination rate and low germination with faster germination rates. These results seemed to coincide with an increase in temperature and day- and night temperature differences (Fig. 3). Variation in both germinability and rate of germination may be pronounced between families within populations (Fig. 2).

Beginning of flowering

Population data for beginning of flowering are plotted in Fig. 4. Most populations had more than one peak of plants beginning with flowering (Fig. 5, left). Whereas the first peaks varied between populations, the last peaks were synchronized between the 151th and 157th day after sowing. Variability within and between populations is shown by the coefficient of variation (cV), range, standard deviation and variation analyses. Mean onset of flowering was later in higher elevation populations and more individuals remained vegetative (Fig. 4 and Table 1). Two groups of populations were evident in the field experiment at Osnabrück: (1) populations from elevation up to 1500 m, in which the

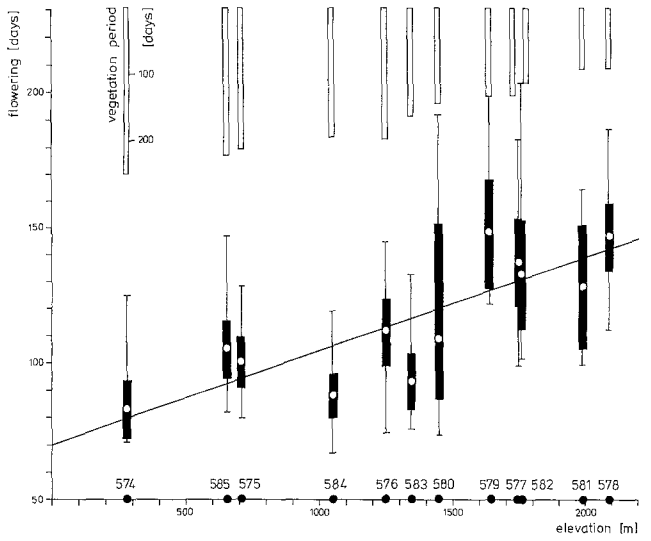

Fig. 4. Onset of flowering in days after sowing: Range (thin lines), standard deviation (thick bars) and population means (o) for each population. The populations are arranged in succession of the altitude gradient of their place of origin ($r=0.84$, $\alpha=0.1\%$). The estimated length of the vegetation periods at the sites of seed collection is indicated on the top of the figure and is defined as the period between daily mean temperature of 7,5° C in spring and 5° C in autumn (Schreiber et al. 1977)

mean onset of flowering was about 74 days after sowing (pop. 574, 576, 580, 583–585) and (2) populations above 1600 m, in which onset of flowering was about four weeks later (pop. 577, 578, 579, 581, 582, Fig. 4).

Plant height

Statistical data for plant height are given in Table 2.

Plant height at the field station in Osnabrück was inversely correlated with elevation of origin (Fig. 6b). However, population variability, judged by the population cV's, increased with elevation of origin (Fig. 6c). This is in accordance with the number of phenotypically similar groups per number of families (LSD-groups, Table 2). Population means of plant height were negatively correlated with beginning of flowering (Fig. 6a). This overall correlation might be misleading. Within some populations, based on family means we observed no significant correlations between plant height and onset of flowering; in others, early flowering was correlated with tall plants and late flowering with small plants, whereas in two populations the opposite trend was observed (Table 4, Fig. 5, middle). The latter two populations, 582 and 584, were the only ones which revealed significant correlations between plant height and rosette diameter (Table 4). When family means for plant height from all populations are plotted against family means for beginning of flowering and rosette diameter, two clusters appear (Fig. 7). Cluster A contained families with plant heights between 35–50 cm and initiation of flowering between 75–110 days after sowing and consisted primarily of families of lowland to submontane origin (pop. 574–576, 583–585, cp. Fig. 1). Cluster B contained families with plant heights of 10–20 cm and flowering times between 130–170 days after sowing and included members of subalpine to alpine origin (pop. 577, 578, 581, 582). Pop. 579 and 580 occupied an intermediate position.

Rosette diameter

Statistical data, ANOVA included, are listed in Table 3. In general early flowering populations has slightly smaller rosette diameters than late flowering ones. This tendency was clearly documented within some populations; significant correlations were obtained between onset of flowering and rosette diameter in pop. 574–576, 582, 584, 585 (Table 4, Fig. 5, right).

Leaf morphology

Based on leaf shape within families, Shull (1911) distinguished four major leaf types ("simplex", "tenuis", "rhomboidea" and "heteris") in *Capsella*. Extensive inheritance studies of leaf shape indicated that a simple genetic system consisting of two Mendelian genes called A and B, each with two alleles, controls the shape and lobing of the rosette leaves. The B-allele at the B-Locus, responsible for leaf forms "heteris" and "rhomboidea", apparently increased with higher elevation (Fig. 6d).

Discussion

The present experiments strengthen the view that variation along the considered plants from a gradient of similar environment is partly due to phenotypic plasticity but is primarily genetically based and correlated with habitat, despite the ease of gene flow via seed transport (Hurka and Haase 1982). The ecological amplitude of *Capsella bursa-pastoris* has a strong genetical component.

Turesson (e.g. 1922a, b, 1930) was the first to show that genetically different populations were often correlated with habitat differences and that similar selected forces appeared to produce similar kinds of adaptations in different species. The term ecotype was applied meaning the product of the genotypic response of a species to its particular habitat. The famous Californian transect experiments by Clausen et al. (1940, 1948; Hiesey 1953) revealed that the investigated species which extended across considerable ranges of the transect, comprised a series of climatic races or ecotypes forming a sequence.

The ecotypes recognized by the Californian workers were based on a large scale. The ecotypes of Turesson were similar in conception but on a smaller scale. Later Clausen (1951) regarded ecotypes as ecological races often composed of a considerable number of local populations, which might be adapted locally thus comparable to the ecotypes of Turesson.

Whereas Turesson and the Californian workers stressed more the discontinuities between the ecotypes, Gregor (1938) showed that ecotype variation was more frequently continuous and he proposed the term ecocline. He redifined the ecotype as a range on an ecocline. Not all genotypic differences between populations will be adaptive. Already Clausen and Hiesey (1958) summarized the variation within the climatic ecotypes of *Potentilla glandulosa:* "In *Potentilla glandulosa* there appears to be both continuous and discontinuous variation. A complete intergradation, or cline, occurs for one character (time of flowering) within one subspecies, whereas other subspecies appear to show random variation for the same character."

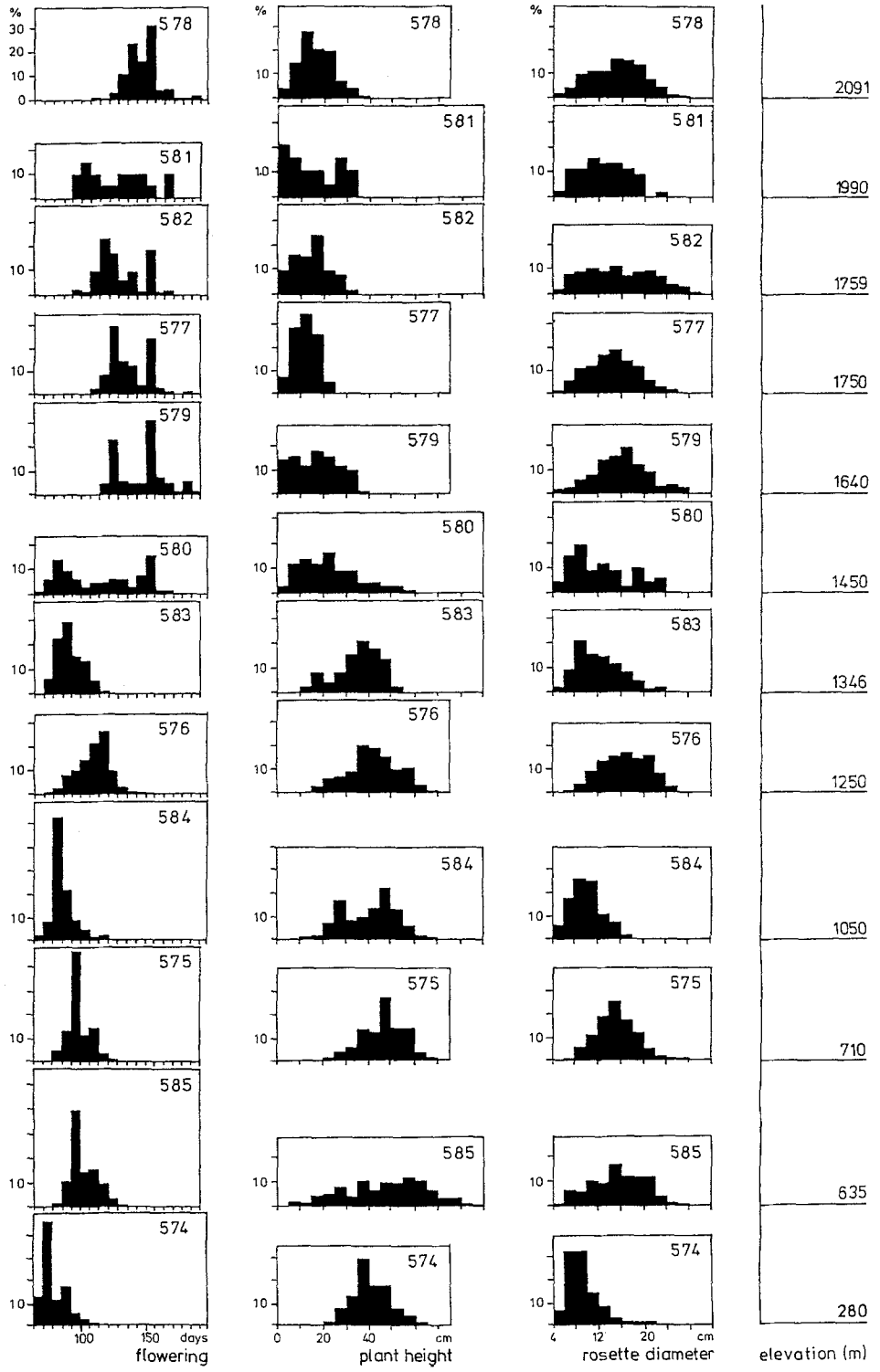

Fig. 5. Frequency diagrams for the number of individuals that begin to flower (left, weekly blocks), plant height (middle, 5 cm blocks), rosette diameter (right, 4 cm blocks). The populations are arranged in accordance with Fig. 4

Random variation within and between populations will be especially pronounced in predominantly self-pollinated and colonising species (Brown and Marshall 1981; Barrett 1982). This turned out to be true for *Capsella bursa-pastoris*. Overall variation patterns revealed macrogeographical patterns superimposed by patchiness which is reflected in very sharp differentiation among some local populations within a geographical region (Hurka 1984). Nevertheless, it has been shown that the expression of important fitness characters varies with the environment (Neuffer and Hurka 1986a and b).

Is it ecotypic variation (adaptive polymorphism) or sufficient phenotypic plasticity to perform well in each of the environments which contribute to the evolutionary success of *Capsella bursa-pastoris*?

Germination. We will first consider germination behaviour. In an extensive study on germination behaviour in *Capsella*, Neuffer and Hurka (1988) provided evidence for genetic heterogeneity between and within populations and concluded that germination of wild *Capsella* plants seems to be regulated by the factors contributing to the inception

Table 1. Within- and between population variability of the onset of flowering (days after sowing)

pop. nr.	*Ni*	*nT* (=%)	$\bar{x}$	cVP	sign. diff.	LSD-groups
574	5	69 (=100)	82	0.129		
585	20	245 (=100)	108	0.099	+	6 out of 18
575	20	248 (=100)	100	0.090	+	5 out of 19
584	17	247 (=100)	87	0.095	+	6 out of 17
576	19	209 (=99.5)	111	0.110	+	8 out of 13
583	16	158 (=100)	93	0.111	+	5 out of 9
580	9	61 (=92.4)	119	0.269	+	3 out of 6
579	17	81 (=50.9)	148	0.137	+	2 out of 5
577	25	251 (=93.7)	138	0.116	+	9 out of 22
582	14	105 (=44.5)	133	0.151	+	2 out of 8
581	4	18 (=43.9)	128	0.175		
578	17	196 (=80)	148	0.085	+	2 out of 13
tot	183	1888	116		+	

Ni = number of families; *nT* = number of flowering individuals, in brackets percentage of the total; $\bar{x}$ = population mean; cVP = coefficient of variability for populations; sign. diff. = significant differences between families (ANOVA, see Methods); LSD-groups = number of homogenous families out of total number which fulfill statistical requirements (LSD-test, see Methods). The populations are arranged in accordance with elevation, see Fig. 4

Table 2. Within- and between population variability of plant height (cm), abbreviations see Table 1; *nT* = number of measured individuals

pop. nr.	*Ni*	*nT*	$\bar{x}$	cVP	sign. diff.	LSD-groups
574	5	68	41	0.199		
585	20	244	48	0.361	+	3 out of 18
575	20	245	48	0.186	+	5 out of 19
584	17	245	42	0.277	+	5 out of 17
576	19	208	43	0.249	+	3 out of 13
583	16	156	36	0.267	−	2 out of 9
580	10	61	24	0.544	+	3 out of 6
579	16	75	19	0.492	+	2 out of 6
577	25	244	13	0.373	+	7 out of 22
582	14	96	16	0.456	−	
581	4	17	17	0.659		
578	17	193	17	0.420	−	
tot.	183	1852	30		+	

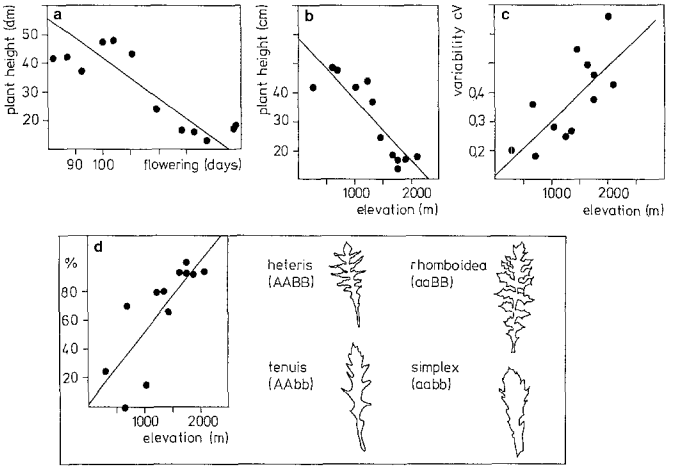

Fig. 6a–d. Correlations and regression lines for the following parameters, based on population means ($n=12$ for all diagrams, cp. Table 4). **a** Plant height: beginning of flowering ($r=-0.85$, $\alpha=1\%$); **b** Plant height: elevation ($r=-0.88$, $\alpha=0.1\%$); **c** Plant height variability: elevation ($r=0.73$, $\alpha=1\%$); **d** Leaf type, percentage of B-allele: elevation ($r=0.81$, $\alpha=1\%$)

and breaking of dormancy, which depend on pre- and post-harvest conditions. They were not able to establish correlations between germinability and environmental patterns. The present results are in accordance with these earlier findings. The observed behaviour (asynchronous and prolonged germination) within and between populations seems to be a sufficient strategy to cope with the unpredictability of both disturbed habitats (Baker and Stebbins 1965; Baker 1974; Barrett 1982) and alpine climates (Franz 1979). It is in full accordance with these arguments that temperature effects play a significant role in terminating dormancy as can be seen from Fig. 3.

Beginning of flowering. The investigated populations exhibited later onset of flowering the higher the altitude of origin (Fig. 4). This was particularly evident in pop- 579: the first individuals began to flower at a time when the growing season at its natural size would have been already finished. A similar response of genotypes along an elevation gradient in the Alps was also found by Neuffer and Hurka (1986a).

The later flowering of alpine populations under lowland conditions possibly relates to low temperature requirements. Growth chamber experiments with varying temperature regimes provided evidence not only for existance of genotypes with and without vernalization requirements but also for genetically based variation in phenotypic plasticity of cold temperature requirements (Neuffer and Hurka 1986a). Our present investigations provide further evidence that alpine populations comprise an array of genotypes with different susceptibility to low temperatures (see least flower peak for pop. 577–580, 582 in Fig. 5). The higher the elevation, the more summer annual genotypes were replaced by winter annual genotypes. This is indicated by the increasing proportion of plants which remained vegetative at the experimental station in Osnabrück (Table 1). The observed tendency to be a winter annual or biennial in alpine populations of *Capsella* fits the general trend in alpine plants.

Plant height. Alpine plants tended to be small (Fig. 5). Variability of plant height between populations increased with

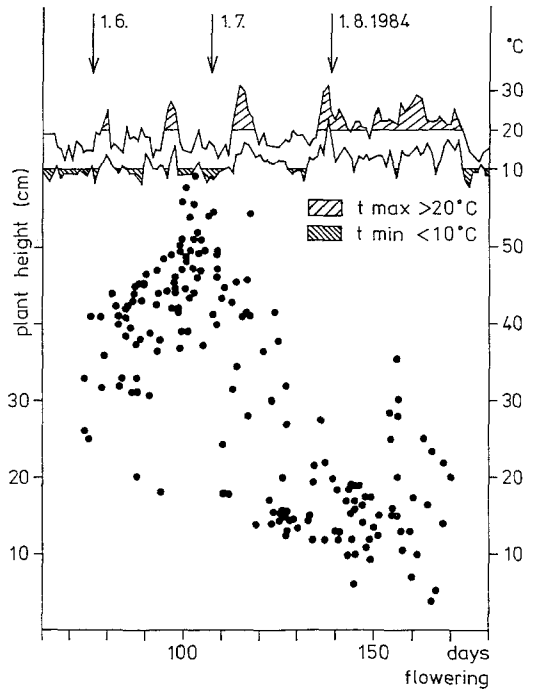

Fig. 7. Correlation diagram for plant height and beginning of flowering. Family means of all populations are plotted. Daily air temperature for Osnabrück values at the top of the diagram

the altitude of origin (Fig. 6c). This may reflect environmental influences; growth conditions during the first half of the experiment (17.5–15.8.1984) were probably more favourable than during the second half which, in general, tends to minimize phenotypic variation. The correlations between plant height and onset of flowering, and rosette diameter and onset of flowering (Fig. 6, Table 4) should be interpreted with caution. They might result from rather complex developmental processes in connection with short and long life spans. In addition, different selection pressures operating on onset of flowering and plant height may interfere.

Compared with alpine populations, populations from Scandinavia are early flowering and did not appear to be

Table 3. Within- and between population variability of rosette diameter (cm), abbreviations see Tables 1 and 2

pop. nr.	*Ni*	*nT*	$\bar{x}$	cVP	sign. diff.	LSD-groups
574	5	65	10	0.334		
585	20	243	16	0.302	+	3 out of 18
575	20	245	16	0.217	+	5 out of 19
584	17	230	11	0.283	+	5 out of 16
576	19	209	17	0.232	+	5 out of 13
583	15	142	13	0.291	+	4 out of 9
580	8	62	13	0.401	+	3 out of 6
579	17	159	17	0.283	+	3 out of 13
577	25	267	15	0.281	+	
582	19	232	16	0.367	+	4 out of 18
581	9	40	13	0.313	–	
578	19	245	16	0.293	–	
tot.	193	2139	14		+	

correlated with elevation (see also Heide 1980, 1982, 1984, 1986a and b, with populations of some species in the *Poaceae* family). They do not need cold treatments for flower initiation (Neuffer and Hurka 1986a). Even when planted in parallel experiments at the experimental station Osnabrück (52.18° N, 8.00° E, 70 m above sea level) and "Schynige Platte" (46.38° N, 8.00° E, 2000 m, Swiss), Scandinavian populations proved to be early genotypes (Neuffer 1986). However, there was a general delay in flowering begin at Schynige Platte for both, Scandinavian and Alpine plants compared to sister plants grown in Osnabrück. This delay may be attributed to different temperatures and/or to photoperiodic effects, since it is known that *Capsella bursa-pastoris* is a quantitative long day plant (Hurka et al. 1976). It is not possible to separate both effects which are influencing one another, unless propriate experiments have been carried out.

Leaf form. Neuffer (1989) demonstrated that expression of genes controlling leaf form and size is easily modified by the environment. Therefore, for a number of leaves, genotypes could not be identified and were not included in the

Table 4. Correlation coefficients (r) and statistical significance

pop.	plant height: flowering			plant height: rosette-diameter			flowering: rosette-diameter		
	n	*r*	sign. diff.	*n*	*r*	sign. diff.	*n*	*r*	sign. diff.
574	5	−0.71	–	5	−0.73	–	5	0.95	+
585	18	−0.25	–	18	0.30	–	18	0.59	+
575	19	0.24	–	19	−0.30	–	19	0.55	+
584	17	0.70	+	16	0.80	+	17	0.76	+
576	13	−0.29	–	13	0.44	–	19	0.50	+
583	16	−0.23	–	9	0.44	–	15	0.47	–
580	10	−0.54	–	6	0.12	–	8	0.56	–
579	16	−0.38	–	7	0.14	–	17	0.21	–
577	22	−0.56	+	22	0.11	–	23	0.15	–
582	13	0.64	+	9	0.70	+	14	0.92	+
581	4	−0.99	+				4	0.24	–
578	13	−0.68	+	13	−0.03	–	17	0.01	–
N	12	−0.85	+	11	−0.20	–	12	0.63	+

(+) indicates significant differences, $\alpha < 5\%$ within and between populations; n = number of families per population; N = number of populations. The populations are arranged in accordance with elevation, see Fig. 4

analysis. There was a pronounced relation between the leaf forms "heteris" and "rhomboidea" and elevation above sea level (Fig. 6d). If the four basic leaf types of *Capsella bursa-pastoris* had no adaptive value, one would expect random distribution (depending on the breeding system) within and between populations. The current as well as previous investigations clearly indicate that this is not the case. Correlations between leaf form and environmental factors such as temperature and rainfall have been clearly established (Steinmeyer et al. 1985). The adaptive significance may be due to physiological and morphological characteristics of the leaf form itself or leaf forms may be linked to other adaptively significant characters.

Ecotypes are the product of the whole environment, but in practice defined with reference to some particular environmental parameters. The ecotype is an experimental category, much more likely to be expressed in physiological rather than morphological differences as Turesson already stressed. The recognition of ecotypic variation may also depend on the characters which are measured. Overemphasis on single characters may confuse rather than clarify the understanding of variation patterns. Our investigation of genecology of *Capsella bursa-pastoris* revealed a very heterogenic pattern which is neither easy to recognize, nor easy to describe. Germination behaviour does not seem to vary in an obvious ecotypic manner, whereas other life history traits such as onset of flowering, plant height and leaf form apparently do.

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