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Colonization history and introduction dynamics of *Capsella bursa-pastoris* (Brassicaceae) in North America: isozymes and quantitative traits

B. NEUFFER and H. HURKA
Department of Systematic Botany, University of Osnabrück, Barbarastraße 11, D-49076 Osnabrück, Germany

Abstract

Multilocus isozyme genotypic composition for aspartate aminotransferase (AAT), leucine aminopeptidase (LAP) and glutamate dehydrogenase (GDH) was studied for *Capsella* in the source continent, Europe (9000 plants from 593 populations), and in the colonized continent, North America (2700 plants from 88 populations). North America was depauperate in the number of genotypes (by ≈ 50%), but in terms of frequencies, a few genotypes were common and shared by both continents. Although some, very rare, genotypes were, however, unique for North America, our data provided no evidence to indicate that the introduced gene pools were reconstructed on a multilocus genetic basis after introduction. Instead, they argued for a considerable number of independent introduction events. Geographical distribution patterns of multilocus genotypes in Europe and North America were pronounced and enabled us to trace the colonization history of Californian *Capsella* back to Spanish ancestral populations and those of temperate North America back to temperate European gene pools. A random-block field experiment with 14 Californian populations from different climatic regions revealed that variation patterns of quantitative traits reflect ecotypic variation, and the ecological amplitude of *Capsella* in North America is similar to that in Europe, which can be traced back to the introduction of preadapted genotypes. It appears that certain multilocus isozyme genotypes are associated with certain ecotypes. The variable European gene pool of *Capsella* was essentially introduced into North America without major genetic changes.

Keywords: *Capsella*, colonization, ecotypes, isozymes, North America

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Introduction

During the last 500 years, human activities have had a tremendous effect on the invasion of non-native species into new habitats, which has led to a crucial change of the biosphere. Information about the extent and mode of biological invasion, and about its ecological and economic importance, are numerous (Elton 1958; Salisbury 1961; Groves & Burdon 1986; Mooney & Drake 1986; Drake *et al*. 1989; di Castri *et al*. 1990; Groves & di Castri 1991; Sukopp 1995). Although plants migrate in large numbers and at high rates between and within continents, introduction dynamics and patterns of migration are mostly known in general terms only. Detailed knowledge of colonization history and migration patterns is still rare but can be detected by analysis of historical records, statistical data evaluation and molecular evidence. Examples are the patterns of weed migration in the northwestern United States (Forcella & Harvey 1988), the introduction dynamics of *Bromus tectorum* L. (Poaceae) in North America (Novak *et al*. 1993; Novak & Mack 1993) and the tracing of ancestral and colonial populations in *Avena barbata* Pott ex Link (Poaceae) (Garcia *et al*. 1989) and in *Capsella bursa-pastoris* (L.) Medik. (Brassicaceae) (Neuffer 1996).

In this study, we will shed light on the colonization history of *C. bursa-pastoris* in North America. *C. bursa-pastoris* has a worldwide distribution, avoiding only the hot and wet tropics. It is one of the most frequent and widespread flowering plants on earth (Coquillat 1951), characterized

Correspondence: H. Hurka. Fax: +49-541-969-3171; E-mail: hurka@biologie.uni-osnabrueck.de

by great colonizing ability and success in almost all man-made habitats. It is mostly a summer- or winter annual, tetraploid and predominantly inbreeding. There is evidence to suggest that *C. bursa-pastoris* originated in Eurasia. It widened its range by following European colonists and established itself as a prominent part of the American weed flora in Post-Columbian times (Hurka & Neuffer 1997). The history of weed introduction into southern and western parts of North America is incidental to Spanish colonization activities; and weed introduction into northern and eastern parts of North America to the colonization activities of the French, the British and other nations. Colonizing plants such as *C. bursa-pastoris* may have been introduced early by Spaniards, or later by Americans or other nationalities, or by both. With the different introductions, different genotypes may have arrived and might have faced different climates.

In this work we studied allozyme variation patterns and life history traits in *Capsella* populations from different geographical and climatic regions of California and other parts of North America, and compared variation in the colonized North American continent with variation in the source continent, Europe. Variation at both the allozyme and the phenotypic level, as expressed by several quantitative traits, reflects colonization history and introduction dynamics of *Capsella* in North America. The role that adaptation may have played in the colonization process is discussed.

Materials and methods

Provenances of Capsella bursa-pastoris samples

The geographical location of the 88 North American population samples and corresponding climatic regions are given in Table 1. The 593 European population samples originated from the Mediterranean region (171 samples), central Europe (291 samples), Scandinavia (75 samples) and the British Isles (56 samples). Information on their country of origin is reported in Table 2.

Isozymes

The following three enzyme systems were assayed: aspartate aminotransferase (AAT; EC 2.6.1.1), glutamate dehydrogenase (GDH; EC 1.4.1.4) and leucine aminopeptidase (LAP; EC 3.4.11.1). Extracts were prepared from 1 g of leaves of single plants. Electrophoresis was performed in a continuous system on polyacrylamide gel slabs. Buffer systems and other experimental details are given in Hurka *et al*. (1989), for AAT, and in Hurka & Düring (1994), for GDH. Isozyme electrophoresis for LAP was as follows: extraction buffer, 0.16 M Tris-HCl, pH 8.0, containing 0.107 M glycine; 7.5% (w/v) polyacrylamide; gel buffer and electrode buffer 0.125 Tris-borate, pH 8.0. Following electrophoresis, the gels were stainied in 0.1 M potassium-phosphate buffer, pH 6.0, containing 0.27 mM L-leucine-β-napthylamide-HCl, 5% (v/v) *N*,*N*-dimethylformamide and 1.2 mM Black-K-Salt.

The genetics of the enzyme systems have been previously studied in *Capsella* (Hurka *et al*. 1989 for AAT, Hurka & Düring 1994 for GDH, Hurka & Neuffer 1997 for LAP). In the present study we adopted the previous nomenclature of the enzyme loci and their allozymes.

Isozyme investigations were carried out on plants raised from seeds collected individually in the wild. All plants were grown in the greenhouse. Rosette leaves of single plants, ≈ 10 weeks old, were harvested and stored at −80 °C. Whenever possible, at least five plants per population sample were assayed for isozyme data. The number of plants analysed per geographical region are given in Tables 2 and 3. Missing data for one or the other enzyme system resulted in varying sample sizes. The multilocus genotypes presented were always for individuals, whether they were given for a single, or for a combination of, enzyme systems. Genotype frequencies are in relation to the corresponding sample sizes, as indicated in the Tables or in the text.

Quantitative traits

Experimental design. Progenies (families) raised from the seeds of mother plants collected individually in the wild were grown in a random-block open-field experiment (carried out from 18 May to 16 July, 1987) in the experimental field of the Botanical Garden of the University of Osnabrück, Germany (geographical coordinates: 52°18′ N, 8°00′ E, 90 m above sea level). Fourteen populations from California, originating from different climatic regions, were analysed (as indicated in Table 1). Seeds were sown in an unheated glasshouse that was not artificially illuminated. The experimental design was to analyse 25 families (= progenies) per population and 10 individuals per family. Different group sizes resulted from either low germination capacity (fewer than 10 individuals in a family), low survival of seedlings or small population sizes (fewer than 25 mother plants per population).

Measured characteristics. The following life-history traits were recorded:

1. FLOW. Onset of flowering. Time from sowing to opening of the first flower bud, as indicated by the appearance of the petals.
2. HEIT. Plant height. The height of the main inflorescence axis at the end of its growing.
3. ROS. Rosette diameter. The maximum diameter measured shortly after the start of flowering.

Table 1 Collection data for the North American populations of *Capsella bursa-pastoris*

Population no.	Country	Locality	Coordinates		Elevation (m)	Climate	Collector
			Latitude N	Longitude W			
341	CDN	Alberta/Elk Island Nat. Park	53°37′	112°45′	650	Df	RH
342	CDN	Alberta/Devon	53°22′	113°44′	650	Df	RH
343	CDN	Alberta/Edmonton	53°33′	113°28′	670	Df	RH
344	CDN	British Columbia/–	—	—	—	—	RH
345	USA	Colorado/Boulder County	40°01′	105°17′	3080	D-E	RH
346	USA	Colorado/Nederland Mt.Res.Station	39°56′	105°30′	2950	D-E	RH
670	CDN	British Columbia/Vancouver	49°16′	123°07′	240	Cs	MB
671	CDN	British Columbia/Vancouver	49°16′	123°07′	240	Cs	MB
674	CDN	British Columbia/Kelowna	49°53′	119°29′	450	Df	MB
675	USA	Missouri/Kansas City	39°05′	94°35′	250	Cf	MB
676	USA	Missouri/Neosho	36°52′	94°22′	350	Cf	MB
677	USA	Missouri/Neosho	36°52′	94°22′	350	Cf	MB
678	USA	Missouri/Neosho	36°52′	94°22′	350	Cf	MB
679	USA	Missouri/Neosho	36°52′	94°22′	350	Cf	MB
680	USA	Missouri/Neosho	36°52′	94°22′	350	Cf	MB
681	USA	Illinois/Chicago	41°53′	87°38′	200	Cf	MB
700	USA	California/Davis	38°32′	121°44′	20	Csa	HH
701	USA	California/Davis	38°32′	121°44′	20	Csa	HH
702	USA	California/Davis	38°32′	121°44′	20	Csa	HH
703	USA	California/Davis	38°32′	121°44′	20	Csa	HH
704	USA	Nevada/Reno	39°30′	119°47′	1350	Ds	HH
705*	USA	California/Davis	38°32′	121°44′	20	Csa	HH
706	USA	California/Davis	38°32′	121°44′	20	Csa	HH
707	USA	California/Davis	38°32′	121°44′	20	Csa	HH
708*	USA	California/Dixon	38°27′	121°46′	20	Csa	HH
709*	USA	California/Woodland	38°41′	121°46′	20	Csa	HH
710	USA	California/Nice	39°06′	122°50′	460	Csb	HH
711*	USA	California/Nice	39°06′	122°50′	460	Csb	HH
712	USA	California/Williams	39°09′	122°09′	25	BS	HH
713	USA	California/near Stockton	37°57′	121°17′	30	Csa	HH
714	USA	California/near Stockton	37°57′	121°17′	30	Csa	HH
715	USA	California/Coulterville	37°43′	120°12′	500	Csb	HH
716*	USA	California/Mariposa	37°29′	119°58′	610	Csb	HH
717	USA	California/near Fresno	36°46′	119°43′	130	BS	HH
718	USA	California/near Fresno	36°46′	119°43′	110	BS	HH
719	USA	California/Pixley	35°58′	119°18′	100	BS	HH
720	USA	California/Delano	35°41′	119°15′	100	BS	HH
721*	USA	California/Shafter	35°25′	119°03′	150	BWh	HH
722	USA	California/Shafter	35°25′	119°03′	150	BWh	HH
723	USA	California/Wheeler Ridge	35°06′	119°01′	150	BWh	HH
724	USA	California/Lancaster	34°42′	118°08′	800	BWh	HH
725*	USA	California/near Lancaster	34°42′	118°08′	710	BWh	HH
726	USA	California/Merced	37°17′	120°31′	50	BS	HH
727	USA	California/Willows	39°31′	122°12′	70	BS	HH
728	USA	California/near Willows	39°31′	122°12′	70	BS	HH
729	USA	California/Chico	39°42′	121°49′	40	BS	HH
730	USA	California/Red Bluff	40°09′	122°15′	100	BS	HH
731*	USA	California/Redding	40°33′	122°23′	150	Csb	HH
732	USA	California/near Weaverville	40°44′	122°56′	600	Csb	HH
733	USA	California/Weaverville	40°44′	122°56′	600	Csb	HH
734	USA	California/Eureka	40°47′	124°09′	20	Csbn	HH
735*	USA	California/near Eureka	40°47′	124°09′	10	Csbn	HH
736	USA	California/near Miranda	40°14′	123°47′	100	Csbn	HH
737	USA	California/near Fort Bragg	39°27′	123°46′	25	Csbn	HH
738	USA	California/near Mendocino	39°19′	123°48′	25	Csbn	HH
739	USA	California/Truckee	39°20′	120°11′	1800	Ds	HH

Table 1 *Continued*

Population no.	Country	Locality	Coordinates		Elevation (m)	Climate	Collector
			Latitude N	Longitude W			
740*	USA	Nevada/Reno	39°30′	119°47′	1340	Ds	HH
741	USA	Nevada/Carson City	39°09′	119°46′	1420	Ds	HH
742*	USA	Nevada/Carson City	39°09′	119°46′	1420	Ds	HH
743*	USA	California/Tahoe City	39°10′	120°08′	1900	Ds	HH
744*	USA	California/Tahoe City	39°10′	120°08′	1900	Ds	HH
745	USA	California/Placerville	38°44′	120°48′	575	Ds	HH
746	USA	California/Davis	38°32′	121°44′	20	Csa	HH
747	USA	California/Truckee	39°20′	120°11′	1800	Ds	HH
748	USA	California/Berkeley	37°57′	122°18′	20	Csbn	HH
749*	USA	California/Sattley	39°37′	120°23′	1500	Ds	HH
750	USA	California/Bucks Lake	39°52′	121°15′	1470	Ds	HH
751	USA	California/San Francisco	37°45′	122°22′	50	Csbn	HH
752	USA	Wyoming/Yellowstone Nat. Park	44°30′	110°35′	2000	Df	HH
785	USA	Missouri/Taos	38°31′	92°03′	200	Cf	KK
786	USA	Missouri/Danville	38°53′	91°27′	200	Cf	KK
846	USA	Missouri/Saint Louis	38°38′	90°11′	130	Cf	BN
847	USA	Missouri/Jefferson City	38°34′	92°10′	200	Cf	BN
848	USA	Missouri/Eureka	38°30′	90°38′	120	Cf	BN
849	USA	Missouri/Hannibal	39°42′	91°22′	150	Cf	BN
850	USA	Oklahoma/Pawnee	36°20′	96°48′	20	Cf	BN
851	USA	Massachusetts/Boston	42°21′	71°04′	20	Df	BN
852	USA	Massachusetts/Boston	42°21′	71°04′	20	Df	BN
853	USA	Massachusetts/Boston	42°21′	71°04′	20	Df	BN
855	USA	Ohio/Columbus	39°57′	83°00′	250	Cf	DC
875	USA	Minnesota/–	—	—	—	—	DC
1357	USA	Alaska/Anchorage	61°13′	149°53′	50	Df	KH
1374	USA	Wisconsin/Milwaukee	43°02′	87°58′	200	Df	UJ
1481	USA	Montana/–	—	—	—	—	FH
1513	USA	Washington D.C.	38°54′	77°01′	20	Cf	CD
1514	USA	West Virginia/Shenandoah	38°29′	78°37′	300	Cf	CD
1515	USA	West Virginia/Shenandoah	38°29′	78°37′	300	Cf	CD
1516	USA	Virginia/Chesapeake Bay Bridge Tunnel	37°00′	76°02′	10	Cf	CD
1517	USA	New York	40°43′	74°01′	20	Cf	CD
1518	USA	New York	40°43′	74°01′	20	Cf	CD
1519	USA	New York	40°43′	74°01′	20	Cf	CD
1520	USA	New York	40°43′	74°01′	20	Cf	CD

Geographical coordinates are given in degree and minutes, elevation in metres (m) above sea level, climates according to the Köppen system (see Hornbeck 1983).
B, dry climates; BS, Steppe climate; BW, desert climate; h, dry-hot; k, cold winter; C, mild, humid climates; f, no dry season; s, dry summer; a, with hot summer; b, with warm summer; n, more than 30 days per year of dense fog; D, snowy-forest climates; f, no dry season; s, dry summer; E, arctic or alpine climates.
*Populations that have been analysed for quantitative traits in addition to isozyme studies.
Abbreviations of collectors: MB, Martin Borgwart; DC, Daniel J. Crawford; CD, Claudia Desmarowitz; RH, Rainer Haase; KH, Klaus Handke; FH, Frank Hellwig; HH, Herbert Hurka; UJ, Uwe Jensen; KK, Katharina Koch; BN, Barbara Neuffer.
CDN, Canada; USA, United States of America.
–, no further specifications are available.

4 PBRA. The number of primary branches, recorded only for one plant per family and determined when HEIT was measured.
5 SBRA. The number of secondary branches, recorded for the same plants as for PBRA and determined when HEIT was measured.
6 FRLE. Fruit length. The mean value of 10 fruits per plant.
7 FRWL. Fruit width. The mean value of 10 fruits per plant, recorded for the same plants as for FRLE.
8 SENU. The seed number per pod as the mean value of 10 pods, recorded for the same plants as for PBRA and determined when HEIT was measured.

Table 2 Number of multilocus genotypes recorded for *Capsella bursa-pastoris* in Europe and North America for the three enzyme systems *Aat*, *Lap* and *Gdh*

	Europe										North America					
	Total		Mediterranean		Central		Scandinavia		British Isles		Total		Californian Central Valley		Other	
Populations	593		171		291		75		56		88		40		48	
Genotypes	N	*n*	N	*n*	N	*n*	N	*n*	N	*n*	N	*n*	N	*n*	N	*n*
Aat	66	8924	23	2675	57	4818	25	1142	11	289	31	2706	5	1642	31	1064
Lap	11	6590	9	2366	10	2783	6	618	3	823	6	2648	3	1508	6	1140
Gdh	6	5515	6	1526	5	2559	4	844	4	386	4	1644	2	1153	4	491

Heterozygotes are omitted.
Aat, aspartate aminotransferase loci; *Gdh*, glutamate dehydrogenase loci; *Lap*, leucine aminopeptidase loci.
n, number of individuals; N, number of genotypes.
Descriptions of geographical regions: Total, sample total; Mediterranean, samples from Egypt, Greece, Israel, Italy, Portugal, Spain, Turkey and the former Yugoslavia; Central, central Europe, samples from Austria, Czech Republic, Denmark, France, Germany, the Netherlands, Poland, Russia (European parts), Slovakia and Switzerland; Scandinavia, samples from Finland, Iceland, Norway and Sweden; British Isles, samples from Ireland and the UK; Californian Central Valley, samples from the Californian Central Valley and adjacent regions with hot summer climates; Other, samples from Canada and the USA outside the Californian Central Valley; see Table 1.

Table 3 Frequencies of *Capsella bursa-pastoris* multilocus genotypes in Europe and North America

		Europe				North America		
Genotypes	Total	Mediterranean	Central	Scandinavia	British Isles	Total	Californian Central Valley	Other
Aat genotypes	*n* = 8924	*n* = 2675	*n* = 4818	*n* = 1142	*n* = 289	*n* = 2706	*n* = 1642	*n* = 1064
1111 1111 1155	0.049	0.020	0.075	0.015	0.038	0.013	–	0.033
1111 1111 3355	0.091	0.035	0.129	0.039	0.176	0.013	–	0.033
1111 1144 1155	0.171	0.385	0.091	0.010	0.148	0.632	0.989	0.070
1111 1144 3322	0.090	+	0.163	0.006	+	+	–	+
1111 1144 3355	0.154	0.039	0.190	0.234	0.318	0.070	+	0.168
1111 1144 5555	0.093	+	0.038	0.554	0.024	+	–	+
1111 1111 0055	0.017	0.058	–	–	–	–	–	–
1122 1144 3355	0.012	+	0.023	+	–	0.028	–	0.071
1144 1111 1155	+	+	+	+	+	0.029	–	0.075
1144 1144 1155	0.122	0.369	0.008	+	0.228	0.016	–	0.043
1144 1111 3355	+	+	–	+	–	0.031	–	0.079
Lap genotypes	*n* = 6586	*n* = 2366	*n* = 2783	*n* = 614	*n* = 823	*n* = 2648	*n* = 1508	*n* = 1140
2255	0.713	0.524	0.841	0.846	0.717	0.406	–	0.942
2266	0.124	0.220	0.026	0.014	0.262	0.011	0.004	0.021
2277	0.114	0.224	0.051	0.104	0.020	0.579	0.991	0.032
Gdh genotypes	*n* = 5515	*n* = 1526	*n* = 2759	*n* = 844	*n* = 386	*n* = 1644	*n* = 1153	*n* = 491
1111 1122	0.606	0.527	0.672	0.629	0.391	0.222	0.030	0.672
1111 2222	0.144	0.383	0.048	0.009	0.179	0.703	0.969	0.079
1111 2233	0.234	0.055	0.269	0.358	0.425	0.059	–	0.197
Aat + *Lap* + *Gdh* genotypes	*n* = 4735	*n* = 1087	*n* = 2750	*n* = 613	*n* = 285	*n* = 1037	*n* = 443	*n* = 594
MMG	0.029	0.126	0.001	–	–	0.423	0.982	0.006

n, number of individuals analysed per isozyme system and per geographical region are indicated at the head of each column. In each case, given frequencies are in relation to the corresponding *n*. Only genotypes with frequencies greater than 0.050 in any of the geographical regions listed are shown.
Aat, aspartate aminotransferase; *Gdh*, glutamate dehydrogenase; *Lap*, leucine aminopeptidase; MMG, Mediterranean multilocus genotype, as defined in the text; +, frequencies less than 0.001; –, not recorded.
For geographical regions see the Table 2 footnote.

9 SEWE. Seed weight as the mean value of 100 seeds, recorded for the same plants as for PBRA and determined when HEIT was measured.

Data analysis

Mean values, range and coefficients of variation (CV) were calculated. As prerequisites for parametric analysis of variance (ANOVA; normal distribution, equal variances) were not fulfilled, a nonparametric ANOVA for unbalanced group numbers was carried out (*H*-test of Kruskal & Wallis). Data were further evaluated by parameter-free correlation analysis (Spearmans ρ) and a principal component analysis (PCA).

Results

Isozyme studies

Compared to the diploid species *Capsella grandiflora* (Fauché & Chaub.) Boiss. and *C. rubella* Reuter, all enzyme loci were duplicated in the tetraploid *C. bursa-pastoris* as the outcome of polyploidization. *C. bursa-pastoris* is characterized by 'fixed heterozygosity', and inheritance of allozymes was disomic. Six AAT isozymes were specified by three different structural gene complexes, each complex forming a single, allelic quadriplex. Four allozymes have been observed for the *Aat1* complex, five for the *Aat2* complex and five for the plastidic *Aat3* complex (Hurka *et al*. 1989; Hurka & Neuffer 1997). Four loci organized in two loci complexes determine the polypeptide structure of the plastidic GDH, which is a homohexameric enzyme. The *Gdh1* complex appeared to be monomorphic whereas the *Gdh2* complex segregated for three allozymes in accordance with Mendelian inheritance (Hurka & Düring 1994; Hurka & Neuffer 1997). Three *Lap* loci complexes, each of two loci, code for the LAP isoenzymes. Loci complexes *Lap1* and *Lap2* could not be resolved adequately, whereas the *Lap3* complex clearly segregated for six alleles (Hurka & Neuffer 1997).

In Europe, nearly 9000 individuals from 593 *C. bursa-pastoris* populations, and in North America ≈ 2700 individuals

Table 4 Frequency of *Capsella bursa-pastoris Aat* multilocus genotypes (N, no. of genotypes in brackets) and individuals (*n*) accounting for them

	Europe		North America	
Frequency classes	Genotypes (N = 66)	Individuals (*n* = 8924)	Genotypes (N = 31)	Individuals (*n* = 2706)
$F < 0.01$	0.697 (46)	0.102	0.612 (19)	0.117
$F \geq 0.01 < 0.05$	0.182 (12)	0.111	0.225 (7)	0.093
$F \geq 0.05 < 0.10$	0.030 (2)	0.066	0.097 (3)	0.088
$F \geq 0.10$	0.090 (6)	0.721	0.064 (2)	0.702

Genotypes were assigned to one of the frequency classes if their frequencies (*F*) reached the corresponding values in at least one of the geographical regions listed in Table 2.
Aat, aspartate aminotransferase.

Table 5 Distribution of the *Capsella bursa-pastoris* Mediterranean multilocus genotype (MMG) in the Mediterranean area. Frequencies refer to the number of populations analysed

	Iberia	Italy	Greece	Israel	Egypt	Total
Populations	65	73	22	4	4	168
with MMG	40	11	3	1	—	55
frequency	0.615	0.150	0.136	0.25	—	0.327

from 88 populations, were analysed for isozyme genotypic composition. Population samples covered a wide geographical area (Tables 1 and 2). The genotypes scored were multilocus genotypes: *Aat* genotypes comprised six loci (*Aat1A* and *1B*, *Aat2A* and *2B*, and *Aat3A* and *3B*), the *Lap* genotypes two loci (*Lap3A* and *3B*) and the *Gdh* genotypes four loci (*Gdh1A* and *1B*, *Gdh2A* and *2B*). In Europe, we recorded a total of 66 different *Aat*, 11 *Lap* and six *Gdh* genotypes compared with 31 *Aat*, six *Lap* and four *Gdh* genotypes in North America. Only genotypes that were homozygous at all loci were included. Heterozygous multilocus genotypes were occasionally observed. Their total frequency was ≈ 5%. Genotypic variability in terms of absolute numbers differed not only between, but also within, the continents (Table 2). This picture, however, has to be greatly modified when considering the frequencies of the genotypes. In Europe, only 20 of the 66 *Aat* multilocus genotypes had frequencies higher than 1% in at least one of the geographical regions listed in Table 2. These genotypes were found in 90% of all individuals analysed in Europe. Only eight *Aat* genotypes had frequencies higher than 5%, and six higher than 10% (Table 4) in at least one of the regions of Table 2. These six genotypes accounted for ≈ 70% of the individuals (Table 4). In North America, a rather similar picture was observed. Twelve of the 31 *Aat* genotypes had frequencies higher than 1% and were found in nearly 90% of all *C. bursa-pastoris* plants studied. Only five *Aat* genotypes had frequencies of higher than 5% in at least one of the regions listed in Table 2, and two higher than 10% (Table 4). The latter two genotypes accounted for ≈ 70% of the individuals (Table 4).

Out of a total of 11 *Lap* genotypes recorded in Europe, only four had frequencies above 5% in one of the regions listed in Table 2. One genotype alone accounted for 71% of the individuals, and two others for ≈ 12% each. In North America, two of the most common European *Lap* genotypes had frequencies of 40% and 58%, respectively (Table 3). Three out of the six *Gdh* genotypes were common in Europe but frequencies varied within the continent. The same three *Gdh* genotypes were also common in North America (Table 3).

The genetic depletion of the Californian Central Valley populations is striking. Plants in that region were nearly fixed for the *Aat* genotype *1111 1144 1155*, for the *Lap* genotype *2277* and for the *Gdh* genotype *1111 2222* (Table 3). The combination of these genotypes within individuals resulted in a multilocus genotype of 12 loci from three different enzyme systems. In Europe, this particular multilocus genotype was nearly exclusively recorded only from the Mediterranean region (Table 3). It will therefore be referred to as the Mediterranean multilocus genotype (MMG). It was mainly found in the Iberian peninsula (Table 5). Its *Aat* genotypic component (*1111 1144 1155*) was also rather common in the British Isles ($F = 0.148$), its *Lap* component (*2277*) in Scandinavia ($F = 0.104$) and its *Gdh* component (*1111 2222*) in the British Isles ($F = 0.179$).

Onset of flowering

Grown in the open-field experiment in Osnabrück with its central European temperate climate regimen, Californian *C. bursa-pastoris* provenances from hot desert climates, Mediterranean hot and Mediterranean warm summer climates (valley populations, V) were early flowering, whereas provenances from cooler/wetter climates (snowy-forest and coastal redwood climates: mountain

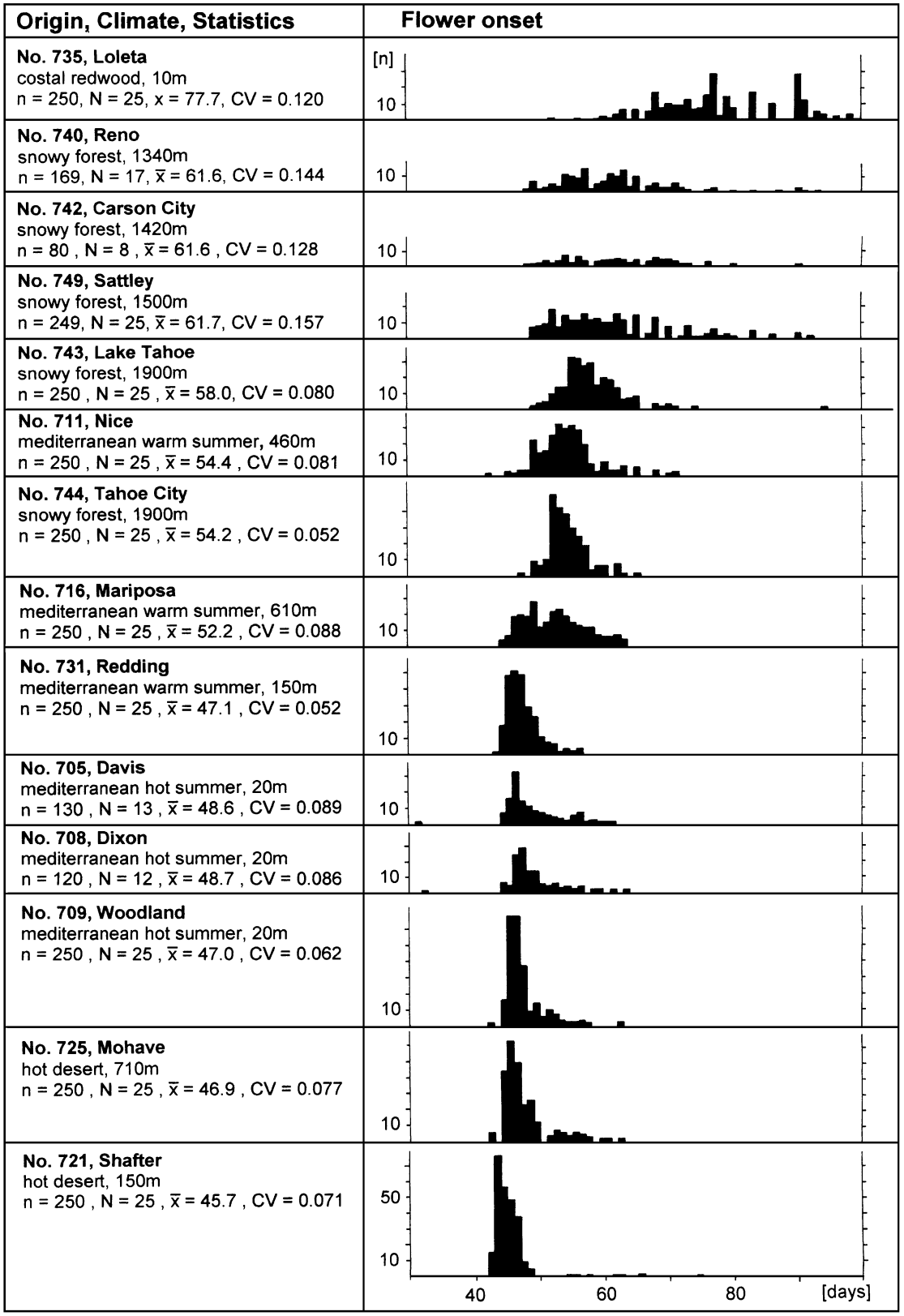

Fig. 1 Flower onset of 14 Californian *Capsella bursa-pastoris* populations in an open-field experiment in Osnabrück, Germany. Population code no., climate, elevation (see Table 1) and statistical parameters are given. *n*, number of total individuals; N, number of progenies; $\bar{x}$, population mean in days to flower onset; CV, coefficient of variability.

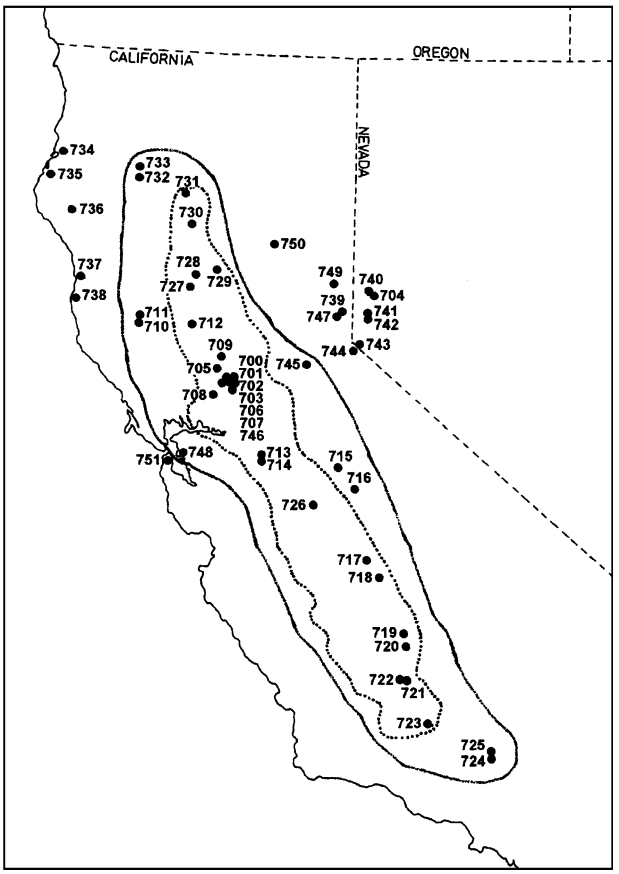

Fig. 2 Geographical distribution of the *Capsella bursa-pastoris* Mediterranean multilocus genotype (MMG) in California. The MMG was only observed within the region encircled by a solid line. The MMG was fixed or nearly fixed in that region. Numbers refer to the population number listed in Table 1. The dotted line surrounds the Californian Central Valley.

populations, M) began to flower later. Variation among families within populations was significant. None of the populations were homogeneous for 'onset of flowering' (*H*-test of Kruskal and Wallis). Within-population variability, as expressed by the range of flower onset and the CV, varied and increased considerably in the M populations (Fig. 1). It would appear from Fig. 2 that there was an association between early flower onset and the MMG, as all early-flowering (but not late-flowering) populations had the MMG. The MMG was also absent in the somewhat intermediate populations 743 and 744, but population 711 had a MMG frequency of 90%.

Statistical analysis

M and V populations differed in their character correlations (Spearman's rank correlation ρ; only ρ-values of > 0.5 were regarded as significant; for M populations $n = 125$, for V populations $n = 173$; measurements are family mean values). Rosette diameter and flowering onset ($\rho = 0.634$ for M and $\rho = 0.705$ for V) and number of seeds per pod and seed weight were positively correlated in both M and V populations ($\rho = 0.813$ for M and $\rho = 0.698$ for V). Branching (primary to secondary, $\rho = 0.535$) and some reproductive characteristics (length of fruit to seed weight, $\rho = 0.503$; width of fruit to number of seeds, $\rho = 0.599$) had distinct correlations in M, but not in V, and rosette diameter and plant height ($\rho = 0.742$), and flower onset and plant height ($\rho = 0.561$) in V, but not in M. There was a tendency for negative correlations between flower onset and seed weight ($\rho = -0.469$) and flower onset and number of seeds per pod ($\rho = -0.399$), in the M populations, whereas these parameters tended to be positively correlated in the V populations ($\rho = 0.458$ and $\rho = 0.366$).

A PCA that included all nine parameters was carried out, separately, for all data (T), for the M populations and for the V populations. Mean values of the families (= progenies) were entered. Three factors were responsible for ≈ 70% of the variability in data sets T and M, and ≈ 65% in data set V (see the legend to Fig. 3). The correlation matrix (Table 6) shows that M and V differed in factor correlations: plant height and rosette diameter were correlated with factor 1 in the V populations, but with factor 2 in the M populations. Primary branching in the M populations was correlated with both factor 1 and factor 3; in the V populations it was correlated with factor 3 only. Fruit width was negatively correlated with factor 1 in M populations, but positively with factor 2 in V populations; seed number per pod and seed weight were negatively correlated with factor 1 in M populations, but positively in V populations. The three factors separated the M from the V populations, as shown in Fig. 3. The M populations were all from Ds and Csbn climates, the V populations from BWh, Csa and Csb climates (see Table 1).

Discussion

Weed introduction to America

The main literature sources of weed introduction to America that we used were: Hornbeck (1983), Krell (1985), Crosby (1986) and Bitterli (1992).

Little is known about weeds in America prior to the 17th century. Mediterranean weeds are thought to be the first successful crossers among colonizing plants, as conquering and colonization of the New World by Europeans started in the West Indies and tropical America, and shipping routes from Europe crossed the 'Mediterranean Atlantic' via the Madeiras, Canaries and Azores. The imported weeds must have taken over large areas in the West Indies, Mexico and other places because Iberian

Table 6 Correlation matrix of the principal component analysis carried out for Californian *Capsella bursa-pastoris* populations marked with an asterisk in Table 1

Parameter	Sample	Factor 1	Factor 2	Factor 3
FLOW	T	**−0.890**	0.235	−0.128
	M	**0.889**	0.197	−0.167
	V	**0.773**	−0.250	−0.164
FLVAR	T	**−0.620**	0.397	−0.114
	M	**0.609**	0.333	−0.248
	V	**0.568**	−0.012	−0.060
HEIT	T	−0.407	**0.673**	−0.346
	M	−0.008	**0.751**	−0.337
	V	**0.754**	−0.300	−0.243
ROS	T	−0.244	**0.726**	0.295
	M	**0.535**	**0.668**	−0.101
	V	**0.824**	−0.300	−0.079
PBRA	T	−0.301	0.179	**0.728**
	M	**0.607**	0.198	**0.594**
	V	0.240	−0.297	**0.769**
SBRA	T	−0.045	0.270	**0.779**
	M	0.421	0.326	**0.713**
	V	0.304	−0.424	**0.629**
FRUL	T	**0.587**	0.444	0.246
	M	−0.330	**0.736**	0.005
	V	0.378	**0.629**	0.243
FRUW	T	**0.851**	0.085	0.330
	M	**−0.747**	0.195	0.352
	V	0.191	**0.701**	0.413
SENU	T	**0.591**	**0.522**	−0.341
	M	**−0.812**	0.340	0.152
	V	**0.629**	0.401	−0.185
SEWE	T	**0.601**	**0.551**	−0.373
	M	**−0.814**	0.394	−0.096
	V	**0.646**	0.387	−0.030

Correlation coefficients greater than 0.5 are given in bold print. For abbreviations of parameters see the text (Materials and methods).
T, total sample; M, mountain populations; V, valley populations. Eigenvalues and explained cumulative variability (percentage, in brackets) are as follows. For T, Factor 1 = 3.274 (32.74); Factor 2 = 2.078 (53.52); and Factor 3 = 1.797 (71.49). For M, Factor 1 = 3.982 (39.82); Factor 2 = 2.158 (61.40); and Factor 3 = 1.231 (73.71). For V, Factor 1 = 3.313 (33.13); Factor 2 = 1.709 (50.21); and Factor 3 = 1.347 (63.68).

conquest created enormous areas of disturbed ground. Mexico's weed flora was, by 1600, probably what it is today: mostly Eurasian with Mediterranean plants predominating.

Despite the rather late colonization of North America, European weeds seem to have already established themselves by the first half of the 17th century. There is a report of several major European weeds, including *Capsella bursa-pastoris* (cited in Crosby 1986), which seems to be the first reference of *Capsella* in North America. California remained one of the most remote regions of any of the European empires until the end of the 18th century, when the Spanish Crown reaffirmed its claim to the Pacific Coast. The first missions were founded in 1769 in San Diego and in 1770 in Monterey. Spanish missionaries and soldiers from Mexico brought with them crop and forage plants, livestock and weeds of the Mediterranean that had colonized Mexico and established themselves, 200 years previously, as a prominent part of the man-made habitats. According to evidence provided by adobe bricks, only three European weeds are thought to have been present prior to colonization in 1769: *Rumex crispus* L., *Sonchus asper* L. and *Erodium cicutarium* (L.) L'Hér. Fifteen alien weeds documented in the adobe bricks are thought to have been introduced into California during the mission period 1769–1824 (Hendry 1931). Although *Capsella* is not among them, this is by no means testimony against its presence in California. It is also not documented in adobe bricks from Mexico, although it had probably been part of Mexico's introduced weed flora since 1600. A number of weeds came into California during the late Spanish era and the Mexican years after 1824, and more with the great hordes of gold seekers. By 1860, at least 90 alien weeds were naturalized, and in the first half of the 20th century, introduced plants constituted more than 60% of the herbaceous vegetation in the grassland types, over 60% in the woodland and over 50% in the chaparral (Robbins 1940). By 1960, the number of naturalized alien plant species in California was estimated at more than 800 (Frenkel 1970).

Introduction dynamics of C. bursa-pastoris

A striking feature of weeds is the founding of populations in new habitats. As the introduction of weeds in hitherto unoccupied areas is mostly accidental, especially when long-distance intercontinental introductions are concerned, an interesting evolutionary question is whether the variation pattern in the newly colonized continent reflects that from the source continent. And, if so, the question arises of whether this goes back to multiple, few or single introductions, and whether ecotypic variation in the colonized continent (given that there is one) can be traced back to the introduction of 'preadapted' genotypes or whether selection for adaptive genetic variation would occur after the introduction.

Molecular evidence and colonization history. A large number of studies—mostly employing isozyme markers—have estimated genetic variability within and among populations of colonizing species (Brown & Marshall 1981; Clegg & Brown 1983; Gray 1986; Barrett & Shore 1989; Barrett & Husband 1990; Hamrick & Godt 1990). Few studies, however, have compared genetic variation in the colonized area with that in the native range. In *Bromus mollis* L. (Poaceae), no differences in the average levels of genetic diversity

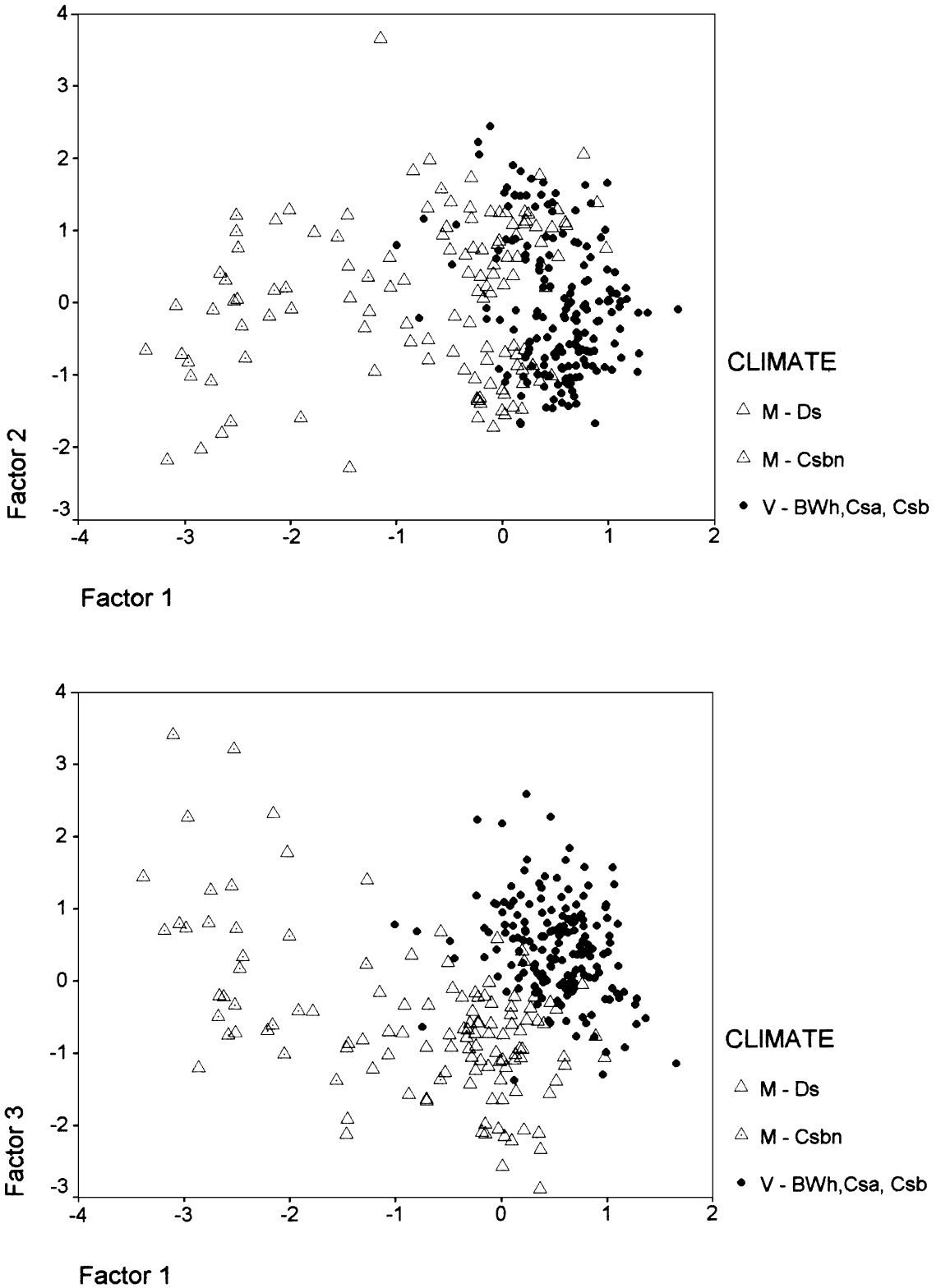

Fig. 3 Factor correlations of the principal component analysis (PCA) for Californian *Capsella bursa-pastoris* populations (marked with an asterisk in Table 1). Mountain populations (M) are from snowy-forest (Ds) and coastal redwood (Csbn) climates. Valley populations (V) are from hot desert (BWh) and Mediterranean dry and warm summer (Csa and Csb, respectively) climates. Measured parameters are given in the text (see the Materials and methods). Eigen values and explained variability (in brackets) are: Factor 1 = 3.274 (32.74%); Factor 2 = 2.078 (20.78%); and Factor 3 = 1.797 (17.97%).

(measured by isozyme markers) between native and introduced populations (England and Australia, respectively) were detected (Brown & Marshall 1981). In *B. tectorum*, however, allelic richness and number of polymorphic loci were higher in its native range (Eurasia and North Africa) than in the introduced North American range, but the level of polymorphism within populations was higher in the introduced range than in the native range (Novak & Mack 1993). A minimum of five or six independent founder events into western North America was postulated (Novak *et al*. 1993). The highly apomictic *Chondrilla juncea* L. (Asteraceae) displayed low clonal variation in Australia but high variation in its native range: three isozyme genotypes found in Australia vs. 91 in Turkey (Chaboudez 1994). Chaboudez argues that the three separate lineages in Australia go back to separate introductions. A comparison of genetic diversity in the introduced and native ranges of the predominantly selfing weed species *Polygonum lapathifolium* L. (Polygonaceae) indicated very low levels of allozyme variation in populations from both North America and Europe (Consaul *et al*. 1991).

Examples cited so far are all from predominantly selfing or apomictic species. However, it is important to consider the mating system when comparing introduced and native populations. Little difference may be found between introduced and native populations of an outbreeding colonizing species. Brown & Burdon (1983) found very high levels of genetic diversity in the annual outbreeding species *Echium plantagineum* L. (Boraginaceae) introduced into Australia, and Kercher & Conner (1996) reported high within- and only moderate between-population variability at isozyme loci in the self-incompatible *Raphanus raphanistrum* L. (Brassicaceae) introduced into North America. Amounts and patterns of genetic variation in the introduced and native ranges (Canada and Europe) of *Apera spica-venti* L. (Poaceae) were consistent with what one would expect in an outcrossing species and do not support the hypothesis of genetically depauperate introductions (Warwick *et al*. 1987).

The present study on *C. bursa-pastoris* covers a wide geographical area in both continents. It appears from our data that when all *Aat*, *Lap* and *Gdh* multilocus genotypes were considered together, eight out of a total of 41 recorded in North America were unique for that continent. However, they accounted only for a very small fraction of the individuals (2% for *Aat*, 0.001% for *Lap*) and were restricted to single populations. Thirty-three genotypes were common to both continents and Europe had a total of 83. It would seem that the colonized continent is genetically depauperate compared with Europe. This is correct in absolute terms, but has to be assessed in terms of frequencies. The general picture in both continents is that a few genotypes are very common and found in $\approx 66\%$ of the plants. Nevertheless, variation within and between the continents is obvious (Table 3). Regarding the complexity of the multilocus associations, the great similarity in the variation patterns between Europe and North America strongly argues for a minimum of 20 independent introduction events into North America. We do not have only many independent introduction events, but apparently several different introduction series. The situation in California is outstanding in this respect. The geographical distribution pattern of the MMG is striking. In Europe, the MMG was only recorded from the Mediterranean area and in North America, only from California. Within California, it was restricted to the regions with Mediterranean climates. The present-day distribution can probably be explained by the Spanish colonization of California. The MMG is widespread in the Iberian peninsula and is also distributed in former Spanish colonies in South America (Neuffer *et al*. manuscript in preparation). Strong support for a colonial–ancestral relationship between Californian and Spanish *C. bursa-pastoris* gene pools also comes from another molecular marker. Overall similarity in random amplified polymorphic DNA (RAPD) markers was greater between Californian valley and Spanish populations than it was between Californian valley and Californian mountain populations (Neuffer 1996). Thus, we face a south–north Mediterranean introduction wave by Spanish and an east–west 'temperate' introduction wave by other European nations.

A Mediterranean-source gene pool was also identified for another Californian weed, *Avena barbata* L. (Poaceae), attributed to Spanish colonization (Garcia *et al*. 1989; Perez Pérez de la Vega *et al*. 1991). Ancestral Spanish and colonial Californian gene pools of *A. barbata* were closely similar in allelic compositions on a locus-by-locus basis, but differed in multilocus associations (Pérez de la Vega *et al*. 1991).

Our data for *C. bursa-pastoris* provide no evidence to suggest that the introduced gene pools have been reconstructed on a multilocus genetic basis after introduction. The different genotypes outside the range of the MMG can easily and sufficiently be explained by introduction of these genotypes from parts of Europe other than the Mediterranean region. Exceptions may be some very rare multilocus genotypes found in North America but not in Europe. Outcrosses between migrants and residents of the recipient populations may occasionally occur, leading to segregation and recombination that produces novel genotypes. The question arises, however, as to how to explain the observed sharp boundaries between the ranges of the MMG and the other genotypes.

Adaptation and the colonization process. It has been shown that in *C. bursa-pastoris*, adaptive strategies, as reflected in variation patterns, depend on the trait under study. Germination behaviour, for instance, comes close to a 'general-purpose genotype' (Neuffer & Hurka 1988; Neuffer

& Bartelheim 1989; Hurka & Neuffer 1991), whereas there is pronounced ecotypic variation in the time of flowering between 'early' and 'late' ecotypes on a macro-geographical scale (Neuffer & Hurka 1986a; Neuffer 1990; Neuffer & Albers 1996). In addition to these marked geographical differences, a strong correlation between the time of flowering and elevation above sea level was observed for populations from European alpine regions (Neuffer & Bartelheim 1989). Ecotypic variation patterns have also been demonstrated for growth-form parameters (Steinmeyer *et al*. 1985; Neuffer & Hurka 1986b; Neuffer & Bartelheim 1989; Neuffer & Albers 1996) and for reproductive capacity (Hurka & Neuffer 1991). *C. bursa-pastoris* also clearly displays ecotypic variation in relation to man-made habitats, i.e. 'biotic ecotypes', compared with 'climatic ecotypes' (Neuffer & Meyer-Walf 1996).

It appears from this study that the ecological amplitude of *C. bursa-pastoris* in North America is similar to that in the source continent, Europe. Geographical distribution patterns of 'early' and 'late' strains in California coincide with climate. Early-flowering V populations were confined to hot desert, steppe and Mediterranean climates (except for regions with fog). Late-flowering M populations, on the other hand, were all from coastal regions with fog (redwood climate) and from the snowy-forest climate. It is reasonable to assume that this variation pattern reflects genotypic response to the environment and hence ecotypic variation, as found in Europe.

The question arises as to whether the ecotypic variation of *C. bursa-pastoris* in North America can be traced back to the introduction of preadapted genotypes, or whether selection for adaptive genetic variation has occurred after the introduction. Introduced species can adapt locally and on a wide range to new habitats. This has been reported for a number of species, e.g. see Warwick & Black (1986) and Warwick (1990) for *Abutilon theophrasti* Medic. (Malvaceae) and some other northward-colonizing weeds in North America; Thébaud & Abbott (1995) for *Conyza* species in Europe; and Weber & Schmid (1998) for *Solidago* species in Europe. The investigations on *A. barbata* are of particular interest because its colonization history in California is similar to that of *C. bursa-pastoris*. It was argued that the main force responsible for the evolutionary change in the colonial populations of *A. barbata* was selection for particular combinations of alleles in response to different environments in California (Pérez de la Vega *et al*. 1991; Garcia *et al*. 1991; Allard *et al*. 1993). In *C. bursa-pastoris*, an array of different multilocus genotypes were observed in climates other than hot desert and Mediterranean. All these genotypes, including the MMG, were also recorded in Europe, providing evidence for multiple introductions instead of rearrangements of a single or few introduced multilocus associations in the colonized continent, as was argued for *A. barbata*.

In *C. bursa-pastoris* we can relate variation at the isozyme level with that at the phenotypic level. Early-flowering ecotypes in *Capsella* were restricted to Mediterranean climates, and coincide with the MMG. It would appear that the MMG is a molecular marker for an early-flowering ecotype. A co-segregation analysis (quantitative trait loci analysis) is presently underway to substantiate this hypothesis (Neuffer & Linde 1999).

In the light of the observed ecogeographical pattern of variation, which seems to reflect ecotypic variation, the role that adaptation has played in the colonization process of *C. bursa-pastoris* has to be discussed. Multiple introductions of genotypes from different climates and sources—Mediterranean genotypes with the Spaniards, an array of Central European genotypes with other nations—appears to be beyond any doubt. However, present-day distribution patterns of these genotypes in California is not in accordance with the spread of the colonizers throughout California. We conclude that natural selection influenced the many—and probably preadapted—introduced genotypes, favouring a specific ecotype that is characterized by the MMG in specific 'Mediterranean' habitats. The observed variation pattern of *C. bursa-pastoris* in California is thus the outcome of both colonization accidents and canalization by natural selection. In *Capsella*, colonization apparently occurred without significant genetic change. The variable European gene pool of *Capsella* was essentially introduced into North America without major genetic alterations.

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Barbara Neuffer studies population biology and the colonization history of *Capsella* using molecular (isozymes and random amplified polymorphic DNAs) and phenotypic markers. She is also investigating hybridization events in plants (*Viola* and *Cardamine*). Herbert Hurka studies the biosystematics of Brassicaceae, including molecular genetics, and is currently concentrating on the population and species level and on the phylography of various taxa.
