J. Plant Res. **106** : 15-24, 1993

Journal of Plant Research

Geographic Differentiation among Populations of *Arabis serrata* Fr. & Sav. (Brassicaceae)

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Geographic variation in morphological traits of thirteen populations of *Arabis serrata* was analyzed to characterize the life history of each particular population in the field. These localities varied in altitude, topography, soil type, humidity, vegetation structure and degree of disturbance. Twelve morphological characters were measured in each plant, and populations were compared using both univariate and multivariate analyses. Populations showed significant differences for most of the traits measured. Principal component analyses revealed a significant differentiation among populations although a continuous variation for some traits was noted. Length of capsules and leaf length of inflorescence's stalks were correlated with the number of frost free days and with temperature, precipitation and number of days of the growing season. The number of rosettes was also correlated with the same variables but negatively. Seed weight was correlated positively with altitude but negatively with temperature and length of the growing season. Populations were also differentiated according to soil conditions and disturbance regimes distinguishing different types of populations : i) populations with many small rosettes, and few heavy seeds per capsule in volcanic soils with low disturbance ; ii) plants with many small seeds and few rosettes in very disturbed localities along asphalt roadways and mountain trails ; and iii) large plants with intermediate seed size and intermediate number of seeds per plant in limestone and serpentine soils under different conditions of disturbance.

Populations of *A. serrata* displayed a complex pattern of differentiation in morphological and life history traits in relation to several biotic and abiotic factors. The quantitative nature of the differences among populations of *A. serrata* observed in the field deserves further studies (e.g., quantitative genetics and phenotypic plasticity) under controlled conditions in order to assess the extent of differentiation within this species complex.

Key words : *Arabis serrata* — Brassicaceae — Ecotypes — Geographic variation — Morphological variation — Population differentiation

Morphological differentiation of species within their geographic distribution has been of considerable interest in the study of the evolution of species (Gould and Johnston 1972 ; Wyatt and Antonovics 1981). Morphometric data from variables measured on a continuous scale are important in generating and testing evolutionary hypotheses and taxonomic hierarchies (Bookstain 1982 ; Reyment *et al.* 1984). Divergence among populations may occur as a result of microevolutionary changes of a different nature in time. These changes in isolated populations in different environments produce individuals with different ecological tolerances to physical factors, resulting in the differentiation of diverse ecotypes. The actual geographical distribution of a species may be reflective of these changes over geological time. Differentiation between populations has received much attention in recent years using different approaches and many distinct taxa (e.g., Antonovics *et al.* 1971 ; Silander and Antonovics 1979 ; Antlfinger 1981 ; Chapin and Chapin 1981 ; Shaver *et al.* 1986 ; Schwaegerle *et al.* 1986 ; Lotz 1990).

The genus *Arabis* (Brassicaceae) in Japan comprises ten species (Ohwi 1965 ; Satake *et al.* 1981). Some species are quite variable, but only the morphological and ecological differentiation of *Arabis lyrata* and *A. gemmifera* have been studied (Ihara 1976). *Arabis serrata* varied in morphology throughout its geographical distribution (Ohwi 1965). Plants of this species are distributed in habitats which differ in soil, humidity, light and degree of disturbance, suggesting that populations of *A. serrata* have differentiated in a complex manner. Moreover, the geological origin of most of the localities derived from the literature available, indicates that populations are established in sites with different histories. Then, *A. serrata* provides several advantages for studying the differentiation among populations at different levels and it is plausible to present different hypotheses about the evolutionary pathways of differentiation of populations of *A. serrata*, taking into account morphological, ecological, genetical and historical factors. This paper, as a serie of papers on differentiation of *A. serrata* (Oyama 1991), describes the variation of plants of this species from thirteen populations across a geographic gradient in order to evaluate the extent of differentiation in morphology and life history traits of each particular population under natural conditions. The ecological amplitude (e.g., phenotypic plasticity and response to environmental gradients) of different populations of *A. serrata* in a common garden experiment is reported elsewhere (Oyama 1991).

Materials and Methods

The species

Arabis serrata Fr. & Sav. (Brassicaceae) is a variable species and four varieties have been described, var. *serrata*, var. *glauca*, var. *japonica* and var. *shikokiana* (Ohwi 1938, 1965 ; Satake *et al.* 1981). This species is distributed mainly in Japan ; *A. serrata* var. *serrata* in Honshu (Mt. Fuji) ; var. *glauca* in Hokkaido and northern Honshu ; var. *japonica* in northern and central Honshu ; and var. *shikokiana* in Shikoku, Kyushu, southwestern Honshu and Korea (Quelpaert Islands) (Ohwi 1965). Populations of this species are established in different habitats : limestone cliffs, serpentine barrens, volcanic soils, mountain trials and along asphalt roadways. This species is an outbreeding perennial plant, forming a vegetative rosette in its first growing season, and a flowering stem up to 40 cm in the same or succeeding growing season. Radical leaves are rosulate, 1.5-7 cm long, 8-15 mm wide, prominently coarse-toothed, narrowed to the relatively long petiole ; leaves (one or both surfaces) are covered with 2- to 4-branched hairs. Flowers are protogynous, white, few to rather many, petals are cuneate-obovate, 6-10 mm long ; capsules (siliques) 3.5-6 cm long, 1.5-2 mm wide ; style 1.5-2 mm long ; seeds 1.2 mm long narrowly winged (Ohwi 1965). Flowering begins in May-June and fruit maturation occurs in late July and August. Some information has been published on this species ; the chromosome numbers of *A. serrata* var. *serrata* (Sakai 1935) and *A. serrata* var. *glauca* (Nishikawa 1985), and a brief description of the life-cycle of *A. serrata* var. *serrata* (Yamazaki and Masuzawa 1985).

Methods

More than forty *A. serrata* populations were located (based on herbarium specimens) and visited throughout its range in Japan during July-August of 1989 and 1990. Unfortunately, several populations of *A. serrata* have already disappeared or have been seriously damaged by human disturbance (K. Oyama, unpublished observations). Thirteen populations were selected from a range of habitat types, soil conditions and availability of plants in the field (Tables 1 and 2). Morphological traits of *A. serrata* were measured in each population trying to cover the four varieties reported in the literature. However, populations will be further referred to by the names of the localities rather than variety names.

To assess the morphological variation and performance of *A. serrata*, different number of plants was observed in each site. Population size varied from population to population. In some cases, due to extremely deep root systems in rock crevices or withered rosettes, few plants with only above ground parts were measured. In other cases (e.g., Honjo or Itoigawa), populations were formed by few plants due to extremely disturbed conditions. Sample sizes varied from 8 to 40 entities per population (Table 2) and in all the cases, with the exception of the population of Mt. Fuji, measured plants accounted for more than 50% of individuals in a particular population. Therefore, sampled plants might be considered as representative of each population. It has been suggested some statistical methods to obtain a reliable sample size (Sokal and Rohlf 1981). However, in most of the cases, these methods result impractical in the field and the estimated values might differ on each particular character. A more simple and *a posteriori* test was calculated in the field using the variance and the coefficient of variation of accumulative consecutive samples. When the variation of the last three consecutive points did not vary more than 5% of the maximum variance value, a sample size was considered sufficient. Unfortunately, however, it was not possible to obtain a complete set of data for all the traits and all the populations. In the most disturbed populations, only seeds (capsules) or leaves were collected for further measurements and experiments (see Oyama 1991). Other plant species associated with *A. serrata* in the same habitats were also sampled (see Appendix) and specimens were deposited at the Kyoto University Herbarium (KYO). The general characteristics of each site were noted and the long-term (1961-1990) average climatic conditions for the study sites were obtained from the Japan Meteorological Agency (JMA) (1991). Number of rosettes (RN), number of rosette leaves (LN), leaf length of the largest leaf (LL), leaf width of the largest leaf (LW), number of inflorescences (IN), leaf length of the largest leaf of the inflorescence stalk (SLL), leaf width of the largest leaf of the inflorescence stalk (SLW), number of capsules (siliques) per plant (CN), length of the longest capsule (CL), number of seeds per capsule (SN) and height of the inflorescence stalks (HE) were measured. Because *A. serrata* presents very small seeds, twenty replicates of one hundred groups of seeds per population were weighed (SW).

The measurements made on plants were arranged in a data matrix indicating the means of plant traits for each population. Because it was not possible to collect a complete set of data for all the populations, different statistical tests were applied in order to detect (and assess) the extent of differentiation among populations. The main trends in variation between localities were summarized using univariate and multivariate analyses. Measurements of each particular trait were compared using one-way analysis of variance (ANOVA) with site of origin as a factor. Whenever a significant difference was found (at $P<0.05$), multiple comparison tests were performed following SYSTAT procedures (Wilkinson 1987). Bartlett's test was applied to test the homogeneity of variances (Zar 1974) and transformations of variables were performed when data were not homoscedastic. For

Table 1. Localities and long-term average climatic data (1940-90) for the nearest metereological stations in which plants of *Arabis serrata* were collected*

Locality	Latitude N	Longitude E	Altitude (m)	Frost free days	Precipitation (mm) annual (growing season)	Length of growing season (days)[a]	Mean Temperature (°C) April-October (annual)
1. Rishiri	44°57.6′	141°12.8′	1700-1800	225.2	1125.0 (599.8)	150-165	12.6 (6.3)
2. Yubari	42°50.4′	142°24.3′	600	246.5	1209.7 (640.4)	130-150	14.2 (7.2)
3. Kurotaki	40°35.7′	140°06.0′	200-300	263.5	1519.3 (1117.1)	184-200	16.5 (10.5)
4. Akkado	39°51.5′	141°47.4′	300	306.5	1256.6 (906.8)	180-190	15.9 (10.4)
5. Hayachine	39°33.4′	141°30.0′	1100	263.0	1250.0 (804.4)	150-165	16.4 (9.8)
6. Komagatake	39°45.5′	140°48.3′	700-800	263.0	1250.0 (804.4)	150-165	16.4 (9.8)
7. Honjo	39°21.7′	140°04.9′	150	266.2	1741.4 (1073.7)	184-194	17.4 (11.1)
8. Atsumi	38°37.3′	139°36.3′	50-100	276.2	1843.4 (939.7)	184-190	18.0 (12.0)
9. Itoigawa	37°04.0′	137°49.4′	50	291.4	2901.1 (1543.5)	184-214	19.3 (13.1)
10. Inamura	36°41.5′	139°24.7′	300	302.7	2306.8 (1463.7)	214-229	19.5 (13.4)
11. Fujido	35°59.6′	138°46.6′	600-700	351.3	1226.3 (1075.5)	184-204	18.8 (12.5)
12. Fuji	35°21.0′	138°45.0′	2400	150.0	1729.0 (419.4)[b]	70-80	−0.4 (−6.7)
13. Tsurugi	33°50.6′	134°6.4′	1700-1800	285.7	2448.2 (2448.2)[c]	125-140	10.1 (4.2)

[a] Length of growing season=Duration of period of plant growth (annual number of days with daily (minimum) normal temperature > 6.0°C)

[b] Precipitation of only six months.

[c] Data from 1941-1970

* Altitudinal differences between the reference stations and sample sites were 200 m in average.

Table 2. Descriptive characteristics of the populations studied and the number of plants (range) measured for different morphological traits of *Arabis serrata*.

Population (Locality)	Type of habitat	Degree of man-made disturbance	Number of individuals
1. Rishiri	Edge of a mountain trail (volcanic area)	Low	30-32
2. Yubari	Edge of a forest (serpentine barren)	High	10-23
3. Kurotaki	Edge of a rural road	High	14-20
4. Akkado	Limestone cliff, shaded and humid	Low	8-12
5. Hayachine	Edge of a mountain trail (serpentine area)	Intermediate	30-40
6. Komagatake	Shaded slope covered by mosses beside a waterfall	Intermediate	12-36
7. Honjo	Open slope along a river	High	8-13
8. Atsumi	Border of a rural asphalt road in a limestone derived rocks	High	23-30
9. Itoigawa	Border of a rural asphalt road in a limestone derived rocks	High	6-30
10. Inamura	Border of an asphalt road	High	31-40
11. Fujido	Limestone cliffs, humid and shaded	Low	16-40
12. Fuji	Volcano crater	Low	23-40
13. Tsurugi	Along mountain trails (serpentine soil)	Intermediate	30

Table 3. Comparison of morphological traits among populations of *Arabis serrata*. Means±1 S.E. are presented. Sample sizes in parentheses.

TRAIT*	POPULATION (Localities)												
	Rishiri	Yubari	Kurotaki	Akkado	Hayachine	Komagatake	Honjo	Atsumi	Itoigawa	Inamura	Fujido	Fuji	Tsurugi
LN	7.9±0.3 (32)	6.0±0.4 (22)	5.7±0.6 (20)	—	8.6±0.5 (30)	—	3.6±0.4 (8)	—	—	5.6±0.2 (31)	9.6±0.5 (20)	6.9±0.5 (23)	6.6±0.3 (30)
LL (cm)	4.2±0.2 (32)	4.5±0.4 (23)	3.2±0.3 (20)	—	3.6±0.2 (29)	4.6±0.3 (22)	4.3±0.2 (8)	2.9±0.2 (28)	2.3±0.2 (6)	9.0±0.5 (32)	6.8±0.6 (16)	2.7±0.2 (23)	—
LW (cm)	1.4±0.06 (31)	1.3±0.08 (17)	1.2±0.1 (20)	—	1.0±0.6 (29)	2.6±0.2 (20)	1.2±0.2 (8)	1.6±0.1 (28)	—	2.0±0.1 (29)	2.0±0.2 (14)	0.9±0.04 (23)	—
SLL (cm)	3.0±0.1 (32)	3.1±0.2 (19)	3.4±0.2 (20)	—	2.8±0.2 (29)	—	4.4±0.4 (8)	—	—	4.7±0.3 (33)	5.5±0.4 (18)	1.9±0.1 (23)	3.1±0.2 (31)
SLW (cm)	1.8±0.1 (31)	0.9±0.04 (17)	1.5±0.1 (20)	—	1.4±0.1 (29)	—	2.8±0.3 (8)	—	—	2.1±0.2 (29)	2.8±0.3 (14)	1.0±0.05 (23)	2.1±0.1 (30)
RN	2.9±0.3 (30)	4.6±0.7 (22)	2.1±1.2 (20)	1.4±0.3 (9)	3.2±1.6 (29)	4.6±0.6 (35)	1.0 (8)	1.6±0.2 (30)	1.5±0.2 (30)	2.7±0.3 (33)	2.2±0.3 (20)	5.3±0.7 (23)	3.3±0.8 (30)
HE (cm)	27.1±1.1 (31)	33.2±1.6 (23)	19.4±1.6 (20)	20.0±2.7 (12)	27.5±1.4 (29)	20.7±0.8 (36)	19.2±1.4 (8)	11.1±0.5 (20)	13.5±0.8 (30)	24.2±1.1 (33)	31.4±1.9 (20)	11.2±0.6 (23)	19.9±1.1 (30)
CN	27.5±4.4 (32)	41.7±8.3 (23)	21.8±7.0 (19)	18.4±5.8 (8)	21.7±2.9 (29)	—	15.9±3.0 (8)	—	—	36.5±6.2 (33)	17.3±3.4 (20)	23.1±4.3 (24)	40.3±8.7 (30)
CL (cm)	—	6.1±0.1 (10)	5.9±0.3 (14)	—	5.3±0.1 (40)	5.5±0.2 (12)	6.2±0.3 (13)	6.2±0.2 (23)	—	7.4±0.1 (40)	7.1±0.2 (40)	4.0±0.1 (40)	—
SN	—	34.4±0.8 (10)	32.9±1.9 (14)	—	23.3±0.5 (40)	27.3±0.8 (12)	29.3±1.6 (13)	32.8±1.5 (23)	—	41.5±0.6 (40)	31.7±1.1 (40)	21.8±0.5 (40)	—
SW (g)	—	2.0±0.1 (20)	1.4±0.01 (20)	1.2±0.1 (10)	1.6±0.02 (20)	1.5±0.01 (20)	1.4±0.05 (20)	1.5±0.02 (20)	1.0±0.05 (10)	1.3±0.02 (20)	1.4±0.01 (20)	3.1±0.02 (20)	2.0±0.01 (20)

— Data not recorded

* See text for abbreviations

Table 4. Comparison of morphological traits among populations of *Arabis serrata* tested with (a) a parametric one-way analyses of variance and (b) non-parametric Kruskal-Wallis test.

Trait[†]	Number of populations	*F* or *H*	P
(a)			
LL[a]	11	24.089	***
LW[b]	10	32.923	***
SLL[b]	9	25.113	***
SLW[c]	9	26.951	***
HE[b]	13	44.754	***
CN[b]	10	2.540	**
CL[b]	8	55.293	***
(b)			
LN	8	52.21	***
RN	8	52.52	***
SLN	9	81.60	***
IN	8	13.10	N.S.
SN	9	149.0	***
SW	14	224.54	***

[†] For traits abbreviations, see text

Variables transformed to : [a]square root ; [b]log ; [c]$1/y^{0.5}$ to make the data homoscedastic.

***$P<0.001$; **$P<0.01$; N.S. $P<0.05$

those variables in which transformations were enable to make the data meet the assumptions of ANOVA, I used a non-parametric method : the Kruskal-Wallis test, analogous to a single classification ANOVA (Zar 1974). Multivariate principal component analyses were conducted to detect differences among populations considering several characters simultaneously. Six characters, which presented homogeneity of variances, and eight populations were used in this analyses.

Correlations between environmental (climatic) factors in each locality and means of morphological traits for each population were done using Spearman non-parametric correlation tests (Zar 1974). These correlations may indicate how some environmental parameters are related with plant's traits in a broad geographical scale. The localities (habitats) visited may also be characterized by their soil conditions and degree of disturbance in a more fine scale. Soil conditions in which plants were found were arbitrarily ranked in the following way : rank 1=limestone rocks (crevices) ; rank 2=surrounded limestone rocks but not in crevices ; rank 3=volcanic soils ; rank 4=serpentine barrens ; rank 5=humus soils. In a similar way, the degree of disturbance (mainly by human activities) was classified in three ranks : high, intermediate and low degree of disturbance. Morphological traits were tested with a non-parametric one-way ANOVA using the ranked soil conditions and the degree of disturbance as factors. Two-way ANOVA (both parametric and non-parametric tests) was not performed because many zero cells distorted the analyses.

Table 5. Multiple comparisons among populations of *Arabis serrata* for some representative morphological traits. Values followed by the same letter did not differ at $P<0.05$.

Population	Trait[a]			
	LL (cm)	HE (cm)	CN	CL (cm)
1. Rishiri	4.2(bc)	27.1(d)	27.5(ab)	—
2. Yubari	4.5(bc)	33.2(e)	41.7(b)	6.1(c)
3. Kurotaki	3.2(b)	19.4(b)	21.8(ab)	5.9(c)
4. Akkado	—	20.0(b)	18.4(ab)	—
5. Hayachine	3.6(b)	27.5(d)	21.7(ab)	5.3(b)
6. Komagatake	4.6(c)	20.7(b)	—	5.5(b)
7. Honjo	4.3(bc)	19.2(b)	15.9(a)	6.2(c)
8. Atsumi	2.9(a)	11.1(a)	—	6.2(c)
9. Itoigawa	2.3(a)	13.5(a)	—	—
10. Inamura	9.0(e)	24.2(c)	36.5(b)	7.4(d)
11. Fujido	6.8(d)	31.4(e)	17.3(a)	7.1(d)
12. Fuji	2.7(a)	11.2(a)	23.1(ab)	4.0(a)
13. Tsurugi	—	19.9(b)	40.3(b)	—

— Data not rocorded.

[a] Abbreviations explained in the text

Results

Morphological differentiation among populations

Univariate analyses

Plants of *A. serrata* showed significant differences among populations for most of the morphological traits (Tables 3 and 4). The main results obtained for each particular trait were as follows :

i) Number of rosettes.——Most of the populations had the potential to produce a certain number of rosettes vegetatively. Three populations, Fuji, Komagatake and Yubari, produced significantly more rosettes than other populations. These populations were collected in different habitats, Fuji in volcanic soils, Komagatake in limestone cliffs and Yubari in serpentine soils. Plants from Akkado, Atsumi and Itoigawa scarcely produced rosettes, and plants from Honjo did not have rosettes in the field.

ii) Leaf length (rosette).——The largest leaves were found in plants from Inamura followed by plants from Fujido and Komagatake. All other populations had smaller leaves differentiated in two groups : one composed by Rishiri, Yubari, Kurotaki, Hayachine and Honjo of which the plants had an intermediate size with a great variation ; and secondly, populations from Atsumi, Itoigawa and Fuji populations which displayed the smallest leaves. Plants from Atsumi and Itoigawa are located in very similar habitats along the Japan Sea side (Table 5).

iii) Height (of the inflorescence stalk).——Most of the populations showed significant differences in heights of inflorescences (Table 5). The largest plants were found in Fujido (also for leaf length) and Yubari populations, followed by Rishiri and Hayachine plants. The smallest values were those of Fuji and Atsumi populations. Other populations had intermediate values.

iv) Leaf length (inflorescence).——The largest leaves were found in Fujido plants, followed by those from Inamura and Honjo. Although these populations are from very different habitats, they had similar rosette sizes. Fujido plants are from a very dark and humid site, Inamura from a very disturbed and open site in the border of an asphalt roadway and plants of Honjo were located along a mountain path. The smallest plants, by far, were found in Mt. Fuji populations. The other populations measured did not differ significantly when compared, even being from very different localities; Rishiri and Yubari from Hokkaido, Kurotaki and Hayachine in Honshu, and Tsurugi from Shikoku.

v) Number of capsules per plant.——This character was less variable among all traits measured. Almost all populations had similar numbers of capsules except for Fujido and Honjo, which had less; Inamura, Tsurugi and Yubari had more capsules than other populations.

vi) Capsule length.——Length of capsules differed among the populations although the variation within populations was very great. The shortest capsules were from Fuji plants. This population also had fewer but larger seeds. Plants from Fujido and Inamura had the largest capsules but both populations differed in the number of capsules per plant.

vii) Number of seeds per capsule.——The highest number of seeds per capsule was found in plants from Inamura. Plants from Fuji and Hayachine had the smallest number of seeds per capsule, although they are from very different habitats. These two populations also showed a lower germination rate (Oyama 1991). Kurotaki plants had a very great variation in number of seeds, along with those from Fujido.

viii) Seed weight.——Plants from Fuji had the heaviest seeds among all populations, followed by plants from Yubari and Tsurugi. The smallest seeds were present in Itoigawa and Akkado populations and other populations had intermediate values within this broad range. Populations from Yubari, Akkado and Itoigawa had a great variation in seed weight within their populations.

ix) Number of inflorescences.——Populations did not differ significantly in this trait. Although plants may produce different number of rosettes, not all rosettes can produce an inflorescence.

Multivariate analyses

Principal component analyses were used to assess the extent of differentiation among populations based on the overall variance of morphological traits. The analysis was performed with six morphological traits of eight populations which met the assumptions of a multivariate analyses. The first four principal components explained 96.8% of the total variance (Table 6). The first principal component is a strong vector, accounting for 68.8% of the total variance. It is determined by leaf length and width of the inflorescence stalk (SLL and SLW), and leaf length of the rosette (LL) in the negative direction and by leaf width of the rosette (LW), capsule length (CL) and height of the inflorescence stalk (HE) in the positive direction (Fig. 1).

Table 6. Cumulative variances of the first principal components and the loadings of six traits on each principal component.

Trait	Eigenvectors			
	1	2	3	4
SLL[a]	−0.935	0.048	0.231	0.117
LL	−0.897	−0.116	−0.348	−0.67
LW	0.863	0.085	0.450	−0.027
SLW	−0.809	0.234	0.173	0.492
CL	0.725	0.561	−0.345	0.180
HE	0.724	−0.483	−0.131	0.469
Cumulative variance (%)	68.8	79.2	88.2	96.8

[a] For abbreviations, see text

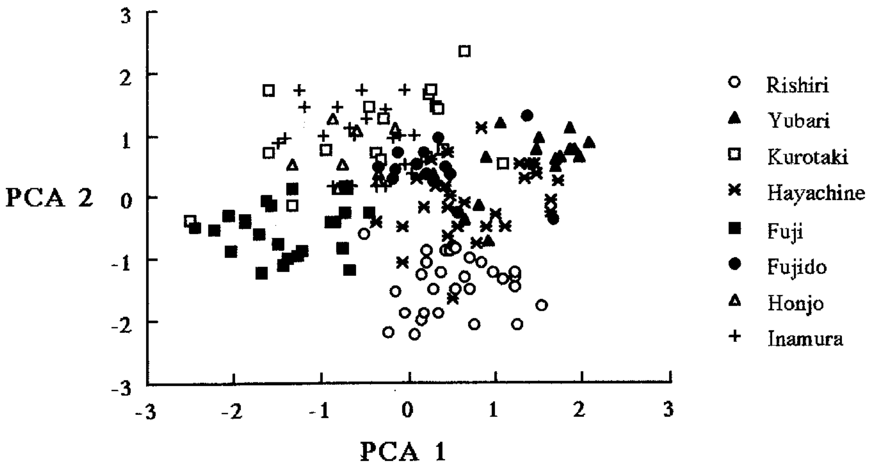

Fig. 1. Differentiation among eight populations of *Arabis serrata* based on the first two principal components calculated from six morphological traits.

Table 7. Differentiation of morphological traits of *Arabis serrata* plants under different soil conditions (a) and distrubance regimenes (b). Means±1 S.E. are presented. Letters followed by the same letter did not differ at $P<0.05$ with a multiple comparison test after a one-way ANOVA. N indicates the number of populations analyzed per trait.

(a)				Soil ranks			
	N	1	2	3	4	5	F[b]
LL[a]	11	6.8±0.6(b)	3.5±0.2(a)	3.5±0.2(a)	4.0±0.2(a)	6.5±0.5(b)	21.343***
RN	13	1.9±0.2(a)	2.3±0.2(a)	3.9±0.4(b)	3.6±0.4(b)	2.2±0.2(a)	7.833***
HE	13	27.1±1.8(c)	14.3±0.5(a)	20.3±1.3(b)	26.3±1.0(c)	22.0±0.8(b)	40.147***
SLL	9	5.5±0.4(c)	—[c]	2.5±0.1(a)	3.0±0.1(a)	4.2±0.2(b)	49.668***
SW	14	1.33±0.03(a)	1.37±0.03(a)	2.01±0.01(d)	1.85±0.03(c)	1.48±0.03(b)	53.568***
CL	9	7.1±0.2(e)	6.0±0.2(c)	4.0±0.01(a)	5.5±0.1(b)	6.8±0.1(d)	76.835***
SN	9	31.7±1.1(c)	30.9±1.1(c)	21.6±0.6(a)	25.5±0.8(b)	37.3±0.9(d)	47.742***
CN	10	17.6±2.9(a)	—	25.6±3.1(a)	34.1±4.2(a)	29.1±4.2(a)	2.247 N.S.

(b)			Disturbance regimenes		
	N	1	2	3	F
LL	11	4.3±0.3(a)	4.1±0.2(a)	5.0±0.3(b)	3.107*
RN	13	3.2±0.3(b)	3.8±0.4(b)	2.2±0.1(a)	14.353***
HE	13	22.9±1.1(a)	22.5±0.7(a)	17.9±0.7(b)	12.991***
SLL	9	3.2±0.2(a)	3.0±0.1(a)	4.0±0.2(b)	9.767***
SW	14	1.60±0.05(b)	1.68±0.08(b)	1.50±0.03(a)	14.189***
CL	9	5.5±0.2(a)	5.4±0.1(a)	6.6±0.1(b)	23.457***
SN	9	26.6±0.9(b)	24.3±0.5(a)	36.0±0.7(c)	68.566***
CN	10	22.9±2.3(a)	31.2±4.8(a)	32.6±3.8(a)	2.312 N.S.

[a] For abbreviations, see text

[b] ***$P<0.05$; *$P<0.05$; N.S. $P>0.05$; [c] data not recorded

Relationships between environmental factors and morphological traits

Some morphological traits were correlated with the environmental variables obtained from the meteorological stations. Leaf length of the inflorescence talks (SLL) and length of capsules (CL) were correlated with the number of frost free days, and temperature, precipitation and length of the growing season [correlation coefficients (r) from $+0.79$ to $+0.91$; $P<0.05$]. The number of rosettes (RN) was negatively correlated with the same environmental variables (r range$=-0.71$ to -0.86 ; $P<0.05$). Seed weight was correlated with length and temperature of the growing season as well as with altitude (r range$=-0.69$; $P<0.01$).

Morphological traits differed among habitats with different soil conditions in a diverse way (Table 7a). Plants established in habitats in limestone cliffs' habitats had larger rosette leaves, inflorescence stalks and capsules, but few rosettes per individual, small seeds and intermediate number of seeds per capsule. Plants from volcanic habitats showed the heaviest seeds and the highest number of rosettes, but few seeds per capsule, and smaller plants. Serpentine plants had intermediate values for most of the traits. Plants from well formed soils had the highest number of seeds per capsule, few ramets per plant and larger rosettes (Table 7a). Most of the traits analyzed in highly disturbed habitats differed from plants from localities with lower disturbance (Table 7b). Plants from disturbed places showed longer rosette leaves but small inflorescence stalks and longer capsules with many seeds. However, these plants had less number of rosettes per plant and smaller seeds.

Discussion

Populations of *Arabis serrata* occur in different habitats with different climatic conditions, types of soils and vegetation, and exposed to different degrees of man-made disturbance. Although the patterns of morphological traits observed in plants of *A. serrata* in the field varied in a continuous manner, it is possible to distinguish different groups of populations differentiated according to the habitats in which plants were found. (i) Several populations of *A. serrata* are living on limestone cliffs with different capacity to live in calcareous soils. In some localities (e.g., Fujido) plants elongate a long primary root to grow between rock crevices with no apparent soil formation. Large plants with intermediate seed size, compared with other populations, are living in these extreme conditions. These habitats are very humid and shaded and density effects by the same or different species are not apparent at the herbal layer. Plants are sparsely distributed where fine crevices appear or ruptures of rocks occur. Most of the populations established on limestone rocks' habitats might have originated in ancient times and at present, remain as small isolated populations restricted to these particular habitats. They may be considered as the oldest populations of this species. (ii) Plants observed in Atsumi, Itoigawa and Honjo are also established in limestone cliffs but they are not directly immersed between limestone rocks but in adjacent places where some superficial soil is formed. Plants are small and produced many small seeds per capsule and few vegetative rosettes. Recent disturbances in these localities by the construction of asphalt roadways may have altered the original habitats and plants of *A. serrata* had to respond to these novel conditions. (iii) A major group of populations could be observed in serpentine rocks at different localities. Plants in Mt. Yubari in Hokkaido or Mt. Hayachine in northern Honshu are some examples. Although both populations are living in the same type of soils, they differed in most of the traits suggesting different patterns of geographic diversification not directly related to the soil conditions. (iv) Other populations had small plants with few large seeds per capsule but with many rosettes produced vegetatively. Plants with these traits have colonized, dispersed and spread vigorously in open, recent volcanic areas as in the Mt. Fuji. Plants are distributed throughout an altitudinal gradient from 1,440 to 2,400 m in this volcano, and the largest population of *A. serrata* observed was in one of its craters. The recent formation of this crater (276 years ago) (Masuzawa 1985) indicates that the changes observed in this population have occurred within this period. Populations from these localities are the most differentiated group of plants within the species (see Oyama 1991). (v) Some populations of *A. serrata* are distributed in a very disturbed habitats (along asphalt roadways) where many weedy species are established in a terrain with soil formation. Plants of *A. serrata* had large rosettes and produced many capsules with many small seeds. Populations like in Inamura may be considered to be formed very recently probably after the openings of roadways forty or fifty years ago.

Most of the morphological traits analyzed may have significant effects on the differentiation of life histories among populations of *A. serrata*. Differences in seed size and number will have different consequences in the performance of plants which are living in very contrasting habitats which differ in the degree of disturbance and stability. For instance, plants from Mt. Fuji had the largest seeds (with dormancy) and the smallest plants (Oyama 1991). It seems that those traits may increase the probability of survivorship and establishment of new seedlings in the short-growing season at higher altitudes like in Mt. Fuji. In contrast, plants from Itoigawa had the smallest seeds which germinate immediately (Oyama 1991) possessing more the features of "weedy" species. Inverse correlations between seed size and seed number between (Primack 1978; Pitelka *et al.* 1983; Marshall *et al.* 1985) and within (Werner 1976) species and within a population (Thompson 1981) are thought to have resulted from selection for large seed size or high seed number when resources are scarce (Harper *et al.* 1970) but with some dependence of the productivity in each particular locality.

Populations of *A. serrata* are located in habitats under different types of vegetation and degree of disturbance. At every site, there is a certain amount of temporal and spatial variation in vegetation structure, and the range of conditions encountered may require different responses (e.g., Van Tienderen 1990). Plant responses depend on the expectation of future development of the vegetation. For example, plants of *A. serrata* living in a very disturbed habitats (e.g., Inamura) grow rapidly in early spring and flower before neighboring plants or weeds cover the herb layer. Although this locality is subjected to constant disturbance (due to maintenance of roadways), mature plants of *A. serrata* grow and reproduce well and apparently, they are not affected by other neighbors during the reproductive period. However, few seedlings were observed in the field suggesting that seedlings must face strong competitive interactions with other plant species during establishment. The degree and frequency of (natural) disturbance may enhance or reduce performance of plants. It is well known also that those neighbors and surrounding vegetation affect growth and reproduction of plant species (Gross 1980; Clay and Shaw 1981; Schwaegerle and Levin 1990; Van Tienderen 1990).

In summary, plants of *A. serrata* have been spread in Japan covering an extensive range of habitats which not only differ environmentally but also historically. A continuous pattern of morphological variation emerged from the observations done in this study and quantitative genetics analyses are required to assess the extent of differentiation among populations in this species (Oyama 1991). On the other hand, differences in life history traits derived from the observations in the field deserve further experimental studies to assess the genetic basis of variation within this species complex.

Many people helped me in different ways during my stay in Japan and I want to express my deeply thanks to all of them. Thanks to S. Kawano for his invitation to visit Kyoto and all the members of the Laboratory of Plant Taxonomy, Department of Botany, Kyoto University for continuous support. Special thanks to G. Murata, H. Nishimura and J. Noguchi for their continuous and disinterested help. Thanks to T. Yahara, H. Tobe, S. Kawano, R. Terauchi and two anonymous reviewers for useful comments on preliminary drafts. Thanks to J. Noguchi, A. Garay, Y. Kohkami, G. Cravioto, H. Shibaike, M.N. Tamura, S. Kinoshita and N. Nakajima for field assistance. To T. Fukuhara, S. Fujii and E. Kinoshita for the identification of plant species. KO was funded by a scholarship of the Ministry of Education of Japan (MONBUSHO). Field work was supported partially by Kyoto University, National University of Mexico and anonymous donations.

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(Received March 16, 1992 : Accepted November 12, 1992)

Appendix. List of plant species associated with *Arabis serrata* populations. Numbers correspond to those listed in Table 1.

1. RISHIRI

*Saxifraga cherleroides*var. *rebunshirensis* (Saxifragaceae), *Betula ermanii* (Betulaceae), *Artemisia arctica*subsp. *sachalinensis* (Asteraceae), *Polygonum bistorta* (Polygonaceae), *Barbarea orthocerae* (Brassicaceae), *Epilobium*sp. (Onagraceae), *Rhodiola ishidae* (Crassulaceae), *Geranium erianthum* (Geraniaceae), *Erigeron thunbergii*subsp. *glabratus* (Asteraceae), *Saxifraga sachalinensis* (Saxifragaceae), *Hypericum kamtschaticum* (Guttiferae), *Aruncus dioicus* (Rosaceae)

2. YUBARI

Trifolium repens (Fabaceae), *Clematis ochotensis* (Ranunculaceae), *Cerastium holosteoides* (Caryophylaceae), *Petasites japonicus* (Asteraceae), *Artemisia montalba* (Asteraceae), *Sorbus*sp. (Rosaceae), *Rumex acetosa* (Polygonaceae)

3. KUROTAKI

Artemisia montana (Asteraceae), *Ixeris dentata* (Asteraceae), *Eupatorium chinenese* subsp. *sachalinensis* (Asteraceae), *Hypericum erectum* (Guttiferae), *Petasites japonicus* (Asteraceae), *Weigela hortensis* (Caprifoliaceae), *Viola grypoceras* (Violaceae), *Wisteria floribunda* (Fabaceae), *Bohemeria tricuspis* (Urticaceae)

4. AKKADO

Artemisia keiskeana (Asteraceae), *Staphylae bumalda* (Staphylaceae), *Cryptotaenia canadensis* (Umbelliferae)

5. HAYACHINE

Betula ermanii (Betulaceae), *Polygonum sachalinense* (Polygonaceae), *Petasites japonicus*var. *giganteus* (Asteraceae), *Artemisia montana* (Asteraceae), *Schizophragma hydrangeoides* (Saxifragaceae), *Sanguisorba officinalis* (Rosaceae), *Viola grypoceras* (Violaceae), *Veronicastrum sibiricum* (Scrophulariaceae), *Astilbe*sp. (Saxifragaceae), *Thalictrum filamentosum*var. *tenerum* (Ranunculaceae), *Picea jezoensis*var. *hondoensis* (Pinaceae).

6. KOMAGATAKE

Acer shirasawanum (Aceraceae), *Acer palmatum*var. *matsumurae* (Aceraceae), *Fagus crenata* (Fagaceae), *Alnus hirsuta* (Betulaceae), *Prunus grayana* (Rosaceae), *Kalopanax septembolus* (Araliaceae), *Cornus controversa* (Cornaceae), *Mentha arvensis* (Labiatae), *Carex reinii* (Cyperaceae), *Celastrus orbiculatus* (Celastraceae), *Synurus pungens* (Asteraceae), *Cirsium* sp. (Asteraceae), *Bohmeria tricuspis* (Urticaceae), *Lindera umbellata* (Lauraceae), *Quercus mongolica*var. *grosserrata* (Fagaceae), *Elastostema umbellatum* (Urticaceae), *Galium triflorifome* (Rubiaceae), *Stellaria alsine*var. *undulata* (Caryophyllaceae), *Schizophragma hydrangeoides* (Saxifragaceae), *Ulmus laciniata* (Ulmaceae), *Petasites japonicus*var. *giganteus* (Asteraceae), *Cacalia hastata* (Asteraceae).

7. HONJO

Aruncus dioicus (Rosaceae), *Hydrangea petiolaris* (Saxifragaceae), *Luzula plumosa*var. *macrocarpa* (Juncaceae)

8. ATSUMI

Oxalis acetosella (Oxalidaceae), *Angelica polymorpha* (Umbelliferae), *Polygonum filiforme* (Polygonaceae), *Zelkova serrata* (Ulmaceae), *Styrax japonica* (Styracaceae), *Acer mono* (Aceraceae), *Bohemeria tricuspis* (Urticaceae), *Fraxinus lanuginosa* (Oleaceae), *Phryma leptostachya* (Phrymaceae)

9. ITOIGAWA Population destroyed.

10. INAMURA

Artemisia montana (Asteraceae), *A princeps* (Asteraceae), *Youngia japonica* (Asteraceae), *Eupatorium chinense* (Asteraceae), *Petasites japonicus* (Asteraceae), *Lactuca raddeana*var. *elata* (Asteraceae), *Deutzia crenata* (Saxifragaceae), *Cardamine flexuosa* (Brassicaceae), *Viola kusanoana* (Violaceae), *Boehmeria nipononivea* (Urticaceae), *Anthriscus aemula* (Umbelliferae), *Oplisemenus undilatifolius* (Poaceae), *Carex stenostachys* (Cyperaceae), *Equisetum arvense* (Equisetaceae)

11. FUJIDO

Euonymus alatus (Celastraceae), *Wisteria floribunda* (Fabaceae), *Phellodendron amurense* (Rutaceae), *Carpinus japonica* (Betulaceae), *Euptelea polyandra* (Euptelaceae), *Sedum aizoon* (Crassulaceae), *Clematis apifolia* (Ranunculaceae), *Acer mono* (Aceraceae), *Dioscorea*sp. (Dioscoreaceae), *Kerria japonica* (Rosaceae), *Zanthoxylum piperitum* (Rutaceae), *Bohmeria tricuspis* (Urticaceae)

12. FUJI

Astragalus adsurgens (Fabaceae), *Polygonum weyrichii* (Polygonaceae), *Carex doenitzii* (Cyperaceae), *Artemisia pedunculosa* (Asteraceae), *Hedysarum viciodides* (Febaceae), *Campanula punctata* (Campanulaceae), *Polygonum cuspidatum* (Polyonaceae), *Solidago virgaurea* (Asteraceae), *Pyrola alpina* (Pyrolaceae), *Astraglaus membranaceus* (Fabaceae), *Calamagrostis hakonensis* (Poaceae), *Maianthemum dilatum* (Liliaceae)

13. TSURUGI Plant species were not recorded. Population collected by H. Shibaike.