ハマハタザオ(アブラナ科)の葉毛の多形現象

J. Phytogeogr. & Taxon.
41 : 55-61, 1993

Ken OYAMA*: Hair Polymorphism in a Local Population of *Arabis stelleri* var. *japonica* (Brassicaceae)

ケン・オヤマ*：ハマハタザオ（アブラナ科）の葉毛の多形現象

Abstract

Variability in leaf hairs is reported for a local population of *Arabis stelleri* var. *japonica* in a sand dune habitat in Toyama Prefecture, Japan. Eleven quadrats (1 m² each) randomly located in a sand dune area (5 quadrats) and in adjacent habitats including a pine forest stand (3) and an intermediate zone between the sand dune and the forest (3) were studied. The proportion of hairy (H) and non-hairy (NH) plants significantly differed among and within these three habitats. Sand dune and ecotonal subpopulations presented, on average, a 3 : 1 (NH : H) ratio. Pine forest stands contained few number of hairy individuals. Hairy and non-hairy plants did not differ in most of the morphological and reproductive traits measured. Patterns of spatial distribution differed between quadrats. Hairy and non-hairy plants were aggregated or randomly distributed. Constancy in presence of leaf hairs in transplanted plants in a common garden suggests that the variance in this character has a genetic component. Hair polymorphism is reported for the first time in this species, and the hairy form should be distinguished from the non-hairy common form as has been done for other species of *Arabis*. Further studies are necessary to understand the ecological and physiological consequences of this polymorphism.

Key words: *Arabis stelleri*, Brassicaceae, hair polymorphism, sand dune, spatial distribution.

The genus *Arabis* in Japan comprises ten species and some of them are very variable morphologically. That is the case of *A. gemnifera* (IHARA, 1976), *A. lyrata* (IHARA, 1976), *A. serrata* (OYAMA, 1991, 1993) and *A. kawasakiana* (OYAMA, unpublished). One of the most notorious morphological trait in this genus is the presence of different type of leaf hairs (*e.g.*, simple, bifurcate or stellate) in one or both leaf surfaces or in stems (OHWI, 1965). This character may vary within a single species in this genus in different ways. For example, in *A. serrata* var. *japonica* most of its populations have leaf hairs in both surfaces although it is possible to find populations with hairs only in the upper surface (OYAMA, 1991, 1993). The variety glauca of *A. serrata* has been distinguished from other varieties by stipitate hairs in its radical leaves (OHWI, 1965). In *A. flagellosa*, the forma *lasiocarpa* has been reported and the only distinguishing trait is the presence of pilose siliques (capsules) in contrast with other formas with none or low density of hairs. In *A. gemnifera*, the forma *alpicola* has been reported, in its northernmost limit, as densely hairy on all parts (OHWI, 1965).

During a research on the population biology of *A. stelleri* var. *japonica* "hamahatazao" in different localities in Japan, I found a sand dune population in Toyama Pref. (Hamakurosaki, Toyama City) which has two types of plants easily distinguishable phenotypically, plants with and without hairs on leaves of both rosettes and inflorescence stalks. Plants of this species are very common in this locality in different habitats from open sand

*Department of Botany, Faculty of Science, Kyoto University, Kyoto 606, Japan 京都大学理学部植物学教室
〒606 京都市左京区北白川追分町
Current address: Centro de Ecología, UNAM, Apartado Postal 70-275, Ciudad Universitaria, Anexo Jardín Botanfco Edterior, Mexfco, 04510, D.F.

dune zones to herb substrate of pine stands. These habitats differed in several micro-environmental and biotic traits. For example, plants in the forest received less light intensity than in open sand dune habitats. Diversity of other plants species also changes throughout these habitats. Plants differ in some morphological and ecological traits (OYAMA, unpublished data) although plant differences related to hair polymorphism in this species are unknown. Hair polymorphism has been suggested to be related to differences in physiological traits related to water economy (e. g., EHLERINGER, 1984) and defenses against herbivores (*e.g.*, LEVIN, 1973). In this report, a comparison in frequency, spatial distribution, morphological and reproductive traits between hairy and non-hairy forms of *A. stelleri* var. *japonica* are presented. The main question addressed in this paper is: which traits are related to differences in hair polymorphism in plants of *A. stelleri* located in a sand dune and adjacent habitats?

Materials and Methods

The locality studied can be divided in three different zones: sand dune, forest and an intermediate ecotonal zone. In each zone, eleven 1 m^2 quadrats (plots) were randomly established along transects. Five quadrats in the sand dune area, three in the forest and three in the ecotone. Plants of *A. stelleri* var. *japonica* in each quadrat were tagged with plastic labels and mapped in scale for further analyses. Scaled maps of each quadrat

TABLE 1. Frequency of hairy and non-hairy forms of *Arabis stelleri* var. *japonica*

Forms	Habitat Dune	Ecotone	Forest	Total	*G*	*P*
Non-hairy	209	244	146	597	432.66	0.001
Hairy	71	86	4	163		
Total	280	330	150	760		

TABLE 2. Ratios between hairy (H) and non-hairy (NH) forms of *Arabis stelleri* var. *japonica*. Chi-square test deviations from a 1 : 1 proportion

	Plots I NH : H	II NH : H	III NH : H	IV NH : H	V NH : H	Total NH : H
1. Dune						
Observed values	58 : 13	59 : 35	32 : 5	34 : 5	26 : 13	209 : 71
Nearest absolute ratios	4 : 1	2 : 1	7 : 1	7 : 1	2 : 1	3 : 1
Chi-square	28.521	7.127	19.703	21.564	4.333	68.014
P	***	*	***	***	*	***
2. Ecotone						
Observed values	120 : 10	48 : 44	76 : 32			244 : 86
Nearest absolute ratios	12 : 1	1 : 1	2 : 1			3 : 1
Chi-square	93.077	0.174	17.926			75.648
P	***	N.S.	***			***
3. Forest						
Obseved values	50 : 0	70 : 0	26 : 4			146 : 4
Nearest absolute ratios	50 : 0	70 : 0	6 : 1			29 : 1
Chi-square	—†	—	16.133			134.427
P	—	—	***			***

†Chi-square test was not applied due to zero values in one of the cells
***$P<0.001$; *$P<0.05$; N.S.$P>0.05$

were divided in 100 cm² subquadrats to estimate the frequencies of plants of each morph, hairy and non-hairy plants, in each subquadrat. The frequency of hairy and non-hairy plants observed in the field was contrasted to a 1 : 1 ratio, to be expected theoretically if there was not any selective pressure against either type of plant; G-test and chi-square statistics were used (ZAR, 1974). Using these frequencies values, the patterns of spatial distribution were also estimated using the Morisita index of aggregation. This index may have values> 1, equal to 1 or <than 1 indicating an aggregated, random or uniform patterns of spatial distribution respectively (POOLE, 1974).

A certain number of plants were collected randomly along line transects in both the ecotone and dune zones. Fifteen non-hairy and 14 hairy plants in the dune zone and 30 plants of each form in the ecotone zone were collected at the beginning of the seeding season. Plants in the forest were not included due to low density of hairy plants. Each plant was measured and separated in its morphological compartments and dried in an oven to 60° C during 24 hours. The following traits were recorded: number of shoots and inflorescences, height of inflorescence stalks, maximum length and width of leaves on the stalks, number of flowers, and shoots, stalks and reproductive biomass.

Several plants of each form (hairy and non-hairy) were collected in the field and they were transplanted into a common garden in Kyoto University, and some were preserved as herbarium specimens (Kyoto University Herbarium). After few weeks, leaves of both types of plants were collected simultaneously to measure the following traits on the same leaves: i) maximum leaf length, ii) maximum leaf width, and iii) leaf hair's density. Leaf length and width were measured from base to tip and at the widest point.

TABLE 3. Patterns of spatial distribution of hairy (H), non-hairy (NH) morphs and all individuals of *Arabis stelleri* var. *japonica*.

	Dune			Ecotone			Forest		
PLOT	NH	H	ALL	NH	H	ALL	NH	H	ALL
I									
I_d†	2.84	2.56	1.97	1.03	—††	1.03	—	—	1.63
F	2.06	1.19	1.69	1.03	—	1.03	—	—	1.31
P†††	***	N.S.	***	N.S.	—	N.S.	—	—	*
Patten ††††	Ag	Ran	Ag	Ran	—	Ran	—	—	Ag
II									
I_d	2.22	2.02	1.81	1.16	1.95	1.65	—	—	2.44
F	1.71	1.35	1.76	1.07	1.45	1.60	—	—	2.01
P	***	*	***	N.S.	***	***	—	—	***
Pattern	Ag	Ag	Ag	Ran	Ag	Ag	—	—	Ag
III									
I_d	2.22	10.0	3.45	2.94	1.51	1.92	1.23	—	1.38
F	1.38	1.36	1.89	2.49	1.15	2.01	1.06	—	1.11
P	**	**	***	***	N.S.	***	N.S.	—	N.S.
Pattern	Ag	Ag	Ag	Ag	Ran	Ag	Ran	—	Ran
IV									
I_d	1.07	—	1.48						
F	1.03	—	1.19						
P	N.S.	—	N.S.						
Pattern	Ran	—	Ran						
V									
I_d	2.77	6.41	2.70						
F	1.45	1.66	1.65						
P	**	***	***						
Pattern	Ag	Ag	Ag						

† I_d=Morisita's Index
†† Data not recorded because a low sample size or no data
††† ***$P<0.001$; **$P<0.01$; *$P<0.05$; N.S. $P>0.05$
†††† Ag=aggregated; Ran=random patterns of spatial distribution

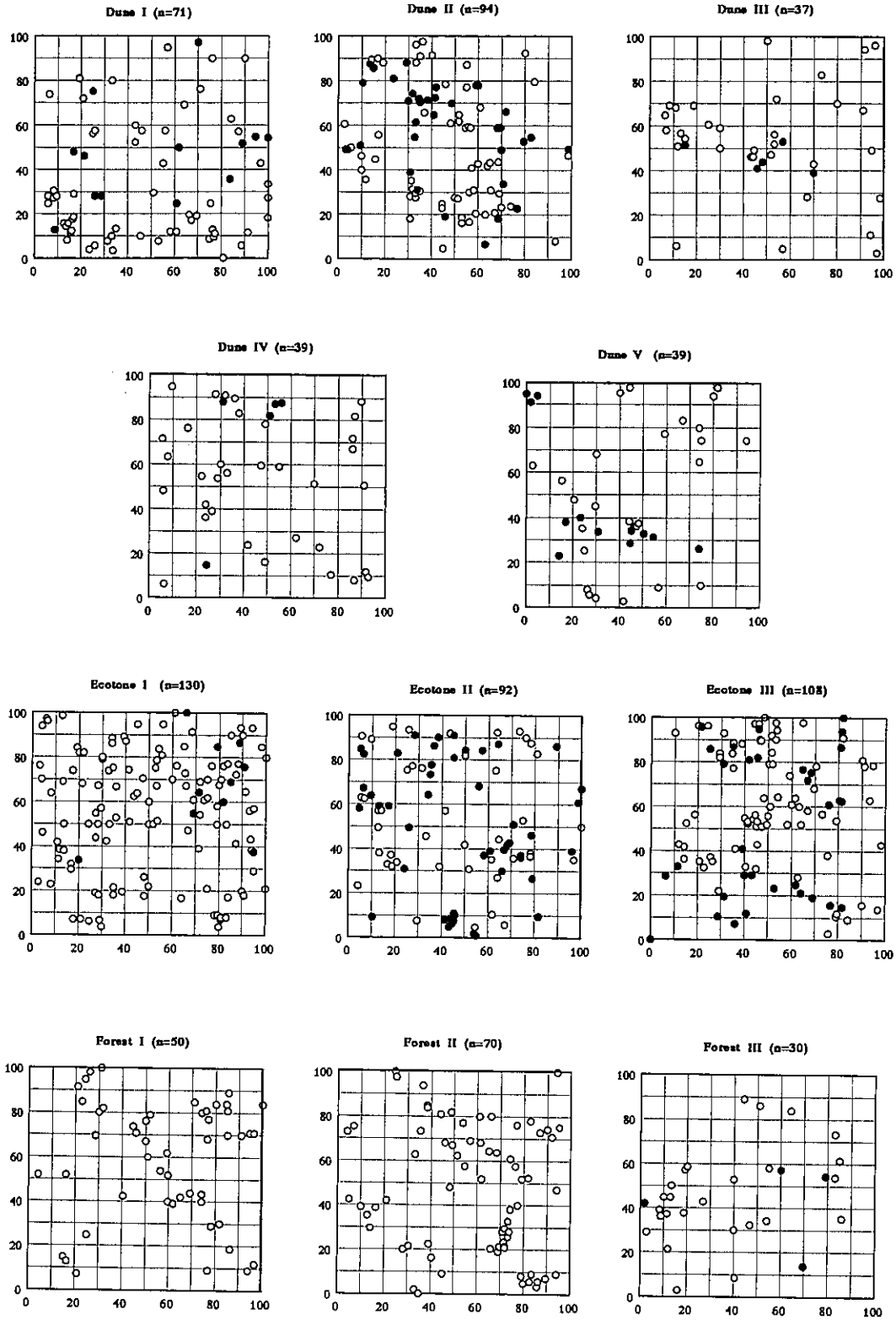

FIG. 1. Spatial distribution of hairy (●) and non-hairy (○) plants of *Arabis stelleri* var. *japonica* in different zones in a sand dune area. Sample sizes in parentheses.

TABLE 4. Comparison between hairy (H) and non-hair (NH) plants of *Arabis stelleri* var. *japonica*.

Trait	Dune		Ecotone	
	H (n=14)	NH (n=15)	H (n=30)	NH (n=30)
Shoot number	2.9±0.6	3.4±0.5	2.8±0.5	2.0±0.3
Height of inflorescence(cm)	18.8±1.0	18.5±1.6	17.1±0.8	19.5±0.7
Leaf number of stalk	17.2±1.1	16.0±1.4	14.4±0.4	14.7±0.6
Leaf length of stalk (cm)	4.7±0.3	4.9±0.4	2.9±0.1	3.0±0.1
Leaf width of stalk(cm)	2.2±0.1	2.0±0.1	1.4±0.01	1.5±0.1
Reproductive units per shoot	69.1±8.3	79.1±16.8	43.7±4.4	54.3±4.1
Total reproductive units	116.8±23.4	177.1±55.4	65.6±10.3	85.3±11.1
Reproductive weight per shoot (g)	0.09±0.01	0.12±0.03	0.06±0.01	0.08±0.01
Total reproductive weight (g)	0.14±0.03	0.23±0.07	0.09±0.02	0.11±0.02
Inflorescence stalk weight (g)	0.32±0.04	0.37±0.09	0.27±0.03	0.28±0.02
Total stalks weight (g)	0.60±0.15	0.91±0.31	0.37±0.06	0.40±0.05

TABLE 5. Comparison of hairy (H) and non-hairy (NH) leaves of *A. stelleri* var. *japonica*

Traits	Leaves		*t*	*P*†
	H (n=50)	NH (n=40)		
Leaf length (cm)	3.9±1.3	4.1±1.1	0.535	N.S.
Leaf width (cm)	1.8±0.5	2.0±1.7	1.658	N.S.
Hair density ††	73.6±14.7	0.05±13.1	14.73	***

†*** $P<0.001$; N.S. $P>0.05$
†† values transformed to arcsin

Hairs were counted directly using a stereoscopic microscope in two 12.56 mm² sample areas in a central location along the length of the upper surface lamina Statistical tests were done following the procedures in ZAR (1974).

Results

Frequency of hairy and non-hairy plants of *A. stelleri* var. *japonica* differed significantly between zones (Table 1). Plant showed different proportion of non-hairy and hairy plants within each zone (Table 2). In sand dune, proportions ranged from 2 : 1 to 7 : 1, and always non-hairy plants showed higher number of plants. However, the total accumulated data of the five dune plots showed a 3 : 1 ratio. In the intermediate zone, the range was higher, from 1 : 1 to 12 : 1 with higher density of non-hairy plants. The total accumulated value in this zone was also a 3 : 1 ratio. In the forest, few hairy plants were found resulting in a proportion of 6 : 1. These proportions do not indicate a mode of genetic inheritance of hair character but the relative proportions of hairy and non-hairy plants in different habitats.

Plants showed aggregated or random patterns of spatial distribution differing among habitats and plots (Table 3, Fig. 1). We did not detect a case with a uniform distribution. In the sand dune zone, all the plants showed significantly aggregated patterns in four of the five plots reflecting the pattern of distribution of non-hairy plants. Hairy plants had aggregation in three plots and random distribution in only one plot. One plot was discarded because small sample size biased estimates of distribution patterns. In the intermediate zone, all plants had aggregated patterns in two plots. Non-hairy plants were randomly distributed in two plots and hairy plants in one. I discarded again one plot because the small number of hairy plants. In the forest, only one plot had few hairy plants and statistical analyses were not performed. Two plots in the forest had aggregated patterns and in

one plot plants were randomly distributed.

Hairy and non-hairy plants did not differ in most of the traits analyzed in both dune and intermediate zones (Table 4). Height of the inflorescence stalk was the only significant difference between both forms of *A. stelleri* in the ecotone zone ($t=2.176$; $P<0.05$). Non-hairy plants had larger stalks' inflorescences than hairy plants.

Leaves differed in density of hairs but leaf length and width did not differ statistically (Table 5). This indicates that similar leaves in size may differ in hair density.

Discussion

Hairy and non-hairy plants of *A. stelleri* var. *japonica* did not differ in most of the traits analyzed. Non-hairy plants were more common in the ecotone and sand dune zones than hairy plants but with a great variation in their relative proportions. Hairy plants also tended to be aggregated rather than regularly distributed. The causes of this aggregation are unknown but it is interesting to observe that hairy plants are more abundant in open conditions. Variation in leaf pubescence has been observed along aridity gradients (e.g., JOHNSON, 1975; EHLERINGER, 1984), temporally (e.g., EHLERINGER and BJORKMAN, 1978) and within individual plants (e.g., JOHNSON, 1975; CANO-SANTANA and OYAMA, 1992).

Presence of pubescence is a common feature in higher plants (KELSEY *et al.*, 1984) and its adaptive value is generally thought to be related to water economy of plants (EHLERINGER, 1982, 1984; EHLERINGER and BJORKMAN, 1978; RODRÍGUEZ, 1983), photosynthesis (EHLERINGER *et al.*, 1976) and to plant's defense against herbivores (LEVIN, 1973; JOHNSON, 1975; RODRÍGUEZ, 1983; KELSEY *et al.*, 1984). In the case of *A. stelleri*, the differences in abundance of hairy and non-hairy plants in each habitat may suggest that hairy forms are better surviving in open, light exposed conditions than in the forest. In a further study, I found that most of the dead plants of *A. stelleri* in open sand dunes were non-hairy plants. However, whether or not this mortality was statistically associated to hair polymorphism was not tested due to confounding effect of human disturbance occurred in the locality. In open habitats, as an immediate response, hairy plants may kept a higher content of water in their leaves than non-hairy plants (K. OYAMA pers. obs.). However, other reproductive and growth traits did not differ between hairy and non-hairy forms. In this species also, an unidentified miner insect has been observed on leaves of *A. stelleri* (K. OYAMA, pers. obs.) although quantitative data are not yet available to test the defensive role of pubescence in "hamahatazao".

Because leaf hairiness did not change after plants were transplanted into a common garden, it is plausible to think that the variance in leaf pubescence has a genetic component in this species. Therefore, this hairy forma must be distinguish it from the common non-hairy condition as has been done in other *Arabis* species (e.g., *A. flagellosa*, *A. gemnifera*) occurring in Japan (OHWI, 1965).

In conclusion, hair polymorphism in *A. stelleri* var. *japonica* is reported for the first time. Two types of plants can be distinguished by the presence of leaf hairs. Both types are located in sand dune and adjacent habitats although in different densities and patterns of distribution. Hairy plants tend to be aggregated in open habitats. Reproductive and size traits did not differ between hairy and non-hairy plants although man-made disturbance limited and confounded the ontogenetic and/or temporal patterns of variation in this species in its natural habitats.

I wish to express my gratitude to all the members of the Department of Botany, Kyoto University for support. To T. YAHARA and two anonymous reviewers for comments on previous drafts. Special thanks to H. NISHIMURA and J. NOGUCHI for continuous support during my stay in Kyoto University. KO was supported by a grant from the Ministry of Culture and Education (MONBUSHO) Japan and anonymous donations.

References

CANO-SANTANA and OYAMA, K. 1992. Variation in leaf trichomes and nutrients of *Wigandia urens* (Hydrophyllaceae) and its implications for herbivory. Oecologia **92**: 405-409.

EHLERINGER, P.J. 1982. The influence of water stress and temperature on leaf pubescence development in *Encelia farinosa*. Am. J. Bot. **69**:

670-675.

EHLERINGER, P.J. 1984. Ecology and ecophysiology of leaf pubescence in North American desert plants. *In*: RODRÍGUEZ, E., HEALY, P.L. and MEHTA, I. (Eds). Biology and Chemistry of Plant Trichomes, pp. 113-132. Plenum Press, New York.

EHLERINGER, P.J. and BJORKMAN, O. 1978. Pubescence and leaf spectral characteristics in a desert shrub, *Encelia farinosa*. Oecologia **36**: 151-162.

EHLERINGER, P.J., BJORKMAN, O. and MOONEY, H.A. 1976. Leaf pubescence: effects on absorptance and photosynthesis in a desert shrub. Science **192**: 376-377.

IHARA, K. 1976. Mode of local differentiation in *Arabis lyrata* and *A. gemnifera* (Cruciferae) in Japan. J. Fac. Sc. Univ. Tokyo **12**: 1-36.

JOHNSON, H.B. 1975. Plant pubescence: an ecological perspective. Bot. Rev. **41**: 233-258.

KELSEY, R.G., REYNOLDS, G.W. and RODRÍGUEZ, E. 1984. The chemistry of biologically active constituents secreted and stored in plant glandular trichomes. *In*: RODRÍGUEZ, E., HEALEY, P.L. and MEHTA, I. (Eds). Biology and Chemistry of Plant Trichomes, pp. 187-241. Plenum Press, New York.

LEVIN, D.A. 1973. The role of trichomes in plant defense. Quart. Rev. Biol. **48**: 3-15.

OHWI, S. 1965. Flora of Japan. Smithsonian Institution, Washington, D.C.

OYAMA, K. 1991. Differentiation among populations of *Arabis serrata* (Cruciferae). Ph.D. Thesis. Kyoto University, Japan.

OYAMA, K. 1993. Geographic differentiation among populations of *Arabis serrata* Fr. & Sav. (Brassicaceae). J. Plant Res. **106**: 15-24.

RODRÍGUEZ, E. 1983. Cytotoxic and insecticide chemicals of desert plants. *In*: HEDIN, P.(Ed.) Plant Resistance to Insects, pp. 291-302. American Chemical Society, Washington.

ZAR, J.H. 1974. Biostatistical Analysis. Prentice Hall, Inc. Englewood Cliffs, NJ.

摘　要

日本の富山県の海岸に自生する *Arabis stelleri* var. *japonica*（ハマハタザオ）の集団について，葉毛の変異性を研究した。海岸地帯（5コドラート），海岸に続く松林を含む地帯(3)，海岸と松林の中間地帯(3)の3地帯に任意に位置した11コドラート(各1 m²) について研究した。葉毛を有する植物(H)と有さない植物(NH)の比率はこれらの3自生地間および自生地内において異なっていた。海岸地帯と推移帯とは平均して3：1(NH：H)の比率を示した。松林地帯での葉毛を有する個体の数はきわめて少なかった。葉毛を有する植物と有さない植物は測定されたほとんどの形態学的および生殖的特性について相違がなかった。空間的分布のパターンはコドラート間で異なった。葉毛を有する植物・有さない植物は集合分布を示すかあるいはランダムな分布を示した。温室に移植した植物について葉毛の存在は不変なので，この特性は遺伝的に決定されていると考えられる。葉毛の多形現象はハマハタザオについて初めて示され，この変異性の結果を明らかにするため生理学的研究が示される必要がある。

(received January 25, 1993; accepted June 22, 1993)

○千々布義朗*：ヒレフリカラマツの新産地　Yoshiro CHICHIBU*: Occurrence of *Thalictrum toyamae* HATUS. et OHWI in Nishisonogi Peninsula, Nagasaki Prefecture

1992年5月10日，これまで佐賀県黒髪山の特産（清水，1982）とされていたヒレフリカラマツが長崎県西彼杵郡西海町七釜郷（標本：千々布義朗 Apr. 17, 1993. KANA162265）にも生育しているのを確認した。

長崎県西彼杵半島北西部には石灰質砂岩からなる岩山が各地で見られる。ヒレフリカラマツはこの一角，近接する数個の岩山の壁面に群生している。生育地は標高50 m前後で，周囲に樹林，もしくは近接する岩山があるため陽光が当たりにくく，陰地ないし半陰地となっている。付近にはイワガサ，コバノチョウセンエノキ，キハギ，カノコユリ，それにこれも今回が長崎県内では初めての確認となったシロバナハンショウヅルなどが見られる。

標本用に採集したなかの6個体を計測したところ，茎の全長は18～30 cmで，これまで知られている佐賀県黒髪山産の茎は10～20 cm（清水，1982）であるから，これよりやや大型であった。また，黒髪山産のものは花期が6月（清水，1982）となっているのに対し，西彼杵半島産のものは1992，1993年の観察結果によると4月上旬～5月上旬であった。特に1993年4月17日，生育地を訪れたときは花の盛りであった。