

# カワラヨモギとオトコヨモギ(キク科)の自然雑種集団とその生物学的位置

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Shoichi Kawano\*, Yukio Nagai\*\* and Seiko Hoshiya-Ushida\*\*\* :  
A Study on the Natural Hybrid Swarms of Two  
*Artemisia* Species, *A. capillaris* and *A. japonica*  
(Compositae) in Central Honshu, Japan, with Special  
Reference to its Biological Status

河野昭一\*・長井幸雄\*\*・星谷-牛田誠子\*\*\* : カワラヨモギと  
オトコヨモギ (キク科) の自然雑種集団とその生物学的位置

Abstract

Intermediate forms in gross morphology that are assumed to be natural hybrids between *Artemisia capillaris* ( $2n=18:2x$ ) and *A. japonica* ( $2n=36:4x$ ) were found in the sympatric populations developed in the flood plain habitats of several large rivers, including the Jinzu, Jyoganji, and Sho Rivers in Toyama Prefecture, Honshu, Japan. All 27 karyologically examined individuals intermediate in gross morphology proved to be triploid ( $3x$ ) with  $2n=27$  somatic chromosomes and also intermediate karyotypes. Meiosis of such triploid plants all showed irregular pairings, including at least two to four univalents and three trivalents. The fertility of triploid pollen was exceedingly low, attaining at most 42.3% on average, with varying diameters and lacking nuclei. The frequent occurrence of diploid or tetraploid plants with somewhat intermediate leaf characters and exceedingly low pollen fertility in sympatric populations of the two *Artemisia* species suggests the possibility of heterogamy by partial backcrosses between triploid hybrids and parental diploid or tetraploid plants. The biological status of hybrid swarms was also discussed in the light of all available information.

**Key Words:** *Artemisia capillaris*, *Artemisia japonica*, natural hybrid population, triploid.

*Artemisia capillaris* Thunb. ex Murray and *A. japonica* Thunb. ex Murray, both belonging to Section *Capillaris* (Compositae), are common perennial species in Japan. *A. capillaris* mainly occurs in a typical maritime sand dune habitat, whereas *A. japonica* is a species of ruderal habitat developed on the foothills or at the margin of the secondary deciduous forests, mainly consisting of *Quercus serrata*, *Q. acutissima*, *Carpinus laxiflora*, etc., although these two species often grow side by side in the grassy habitats developed on the flood plain of the rivers.

Recently we discovered several sympatric sites of these two closely related *Artemisia* species on the flood plains of several large rivers in Toyama Prefecture, Honshu: the Kurobe, Katakai, Haya-tsuki, Jyoganji, and Sho Rivers (Fig. 1); furthermore, we found there numerous individuals of *Artemisia* which in several gross morphological characters exhibited intermediate features between *A. capillaris* and *A. japonica*.

In this paper, we report the results of detailed analyses on such sympatric populations which comprise a number of hybrid-like individuals

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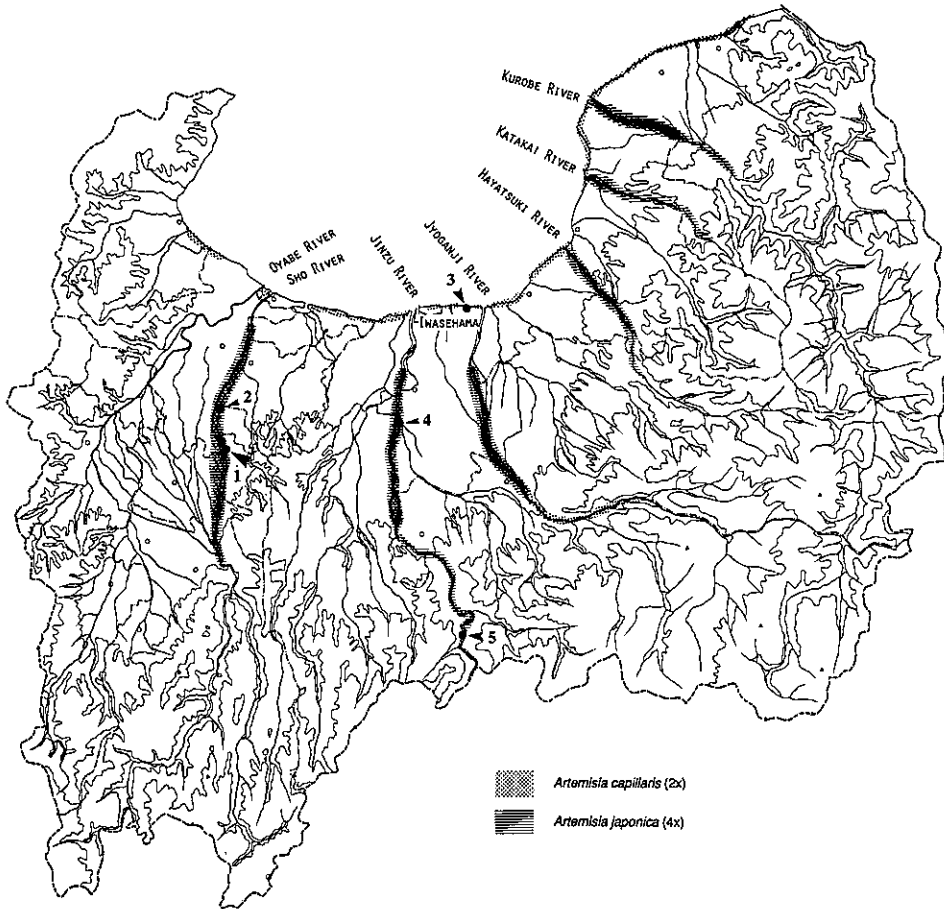


Fig. 1. The distribution ranges of *Artemisia capillaris* and *A. japonica* in Toyama Prefecture, Honshu, Japan. Note that the main ranges of these two species are confined to maritime sand dunes and the flood plains of major rivers in Toyama Prefecture. Arrows specify the research sites: 1. Sho River site; 2, Nakada, Sho River; 3, Iwasehama, Hamakurosaki, Toyama City; 4, Usaka, Jinzu River, Toyama City; 5, Katakake, upper Jinzu River, Nei-gun.

between *A. capillaris* and *A. japonica*. Various characters of *Artemisia* plants, including gross morphology, somatic chromosome numbers and karyotypes, meiotic chromosome pairing, pollen size and fertility of both parental *Artemisia* species, and their putative hybrids, were critically examined. We further discuss the present status of such hybrid swarms occurring in the sympatric populations of these two *Artemisia* species, and its evolutionary implications.

## Materials and Methods

### 1. Field Research Sites and Environmental Factors Surveyed

Sympatric populations of two *Artemisia* species were discovered at several sites on the flood plains of the Jinzu, Sho, Jyoganji, Hayatsuki,

Katakai, and Kurobe Rivers (Fig. 1). In this study, we have selected populations developed on the flood plain of the Sho River for critical analyses from various standpoints. First, one  $3 \times 90$  m belt-transect was established across the east side of the flood plain of the river from the stream to the river bank (Fig. 2). Then, for each of 44 quadrats ( $5 \times 5$  m), all plant species associated with *A. capillaris* and *A. japonica* and their cover degrees, frequencies of *A. capillaris*, *A. japonica*, and their putative hybrids were surveyed.

Soil samples were also taken from 22 plots, each with 5-m intervals, and then the amounts of total carbon and total nitrogen were analyzed with a C-N automatic analyzer (Yanagimoto).

Within the above belt-transect, one  $3 \times 5$  m plot was further established to survey in more detail

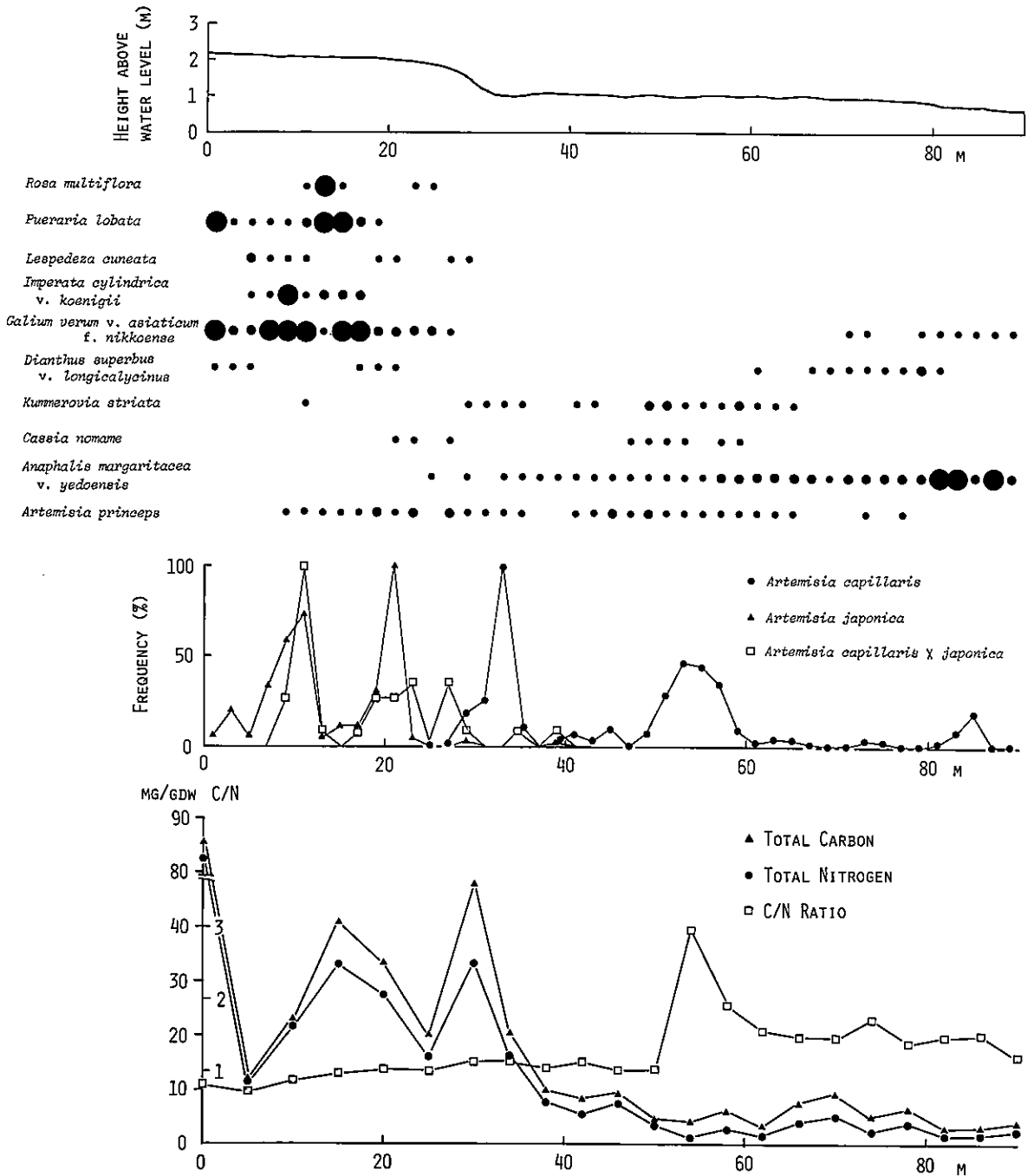


Fig. 2. The diagram illustrating the belt-transect (3 × 90 m) across the flood plain of the Sho River site (see Fig. 1), in which the relative abundance of plant species associated with two *Artemisia* species, *A. capillaris* and *A. japonica*, and putative hybrids between them. Note that *A. capillaris* is more common in wetter sites near the river stream, while *A. japonica* occurs in more interior sites near the river bank. Total carbon, total nitrogen, and C/N ratio in the soil layer of the above transect were examined, and they clearly show the occurrence of a gradient across the transect in these important soil elements.

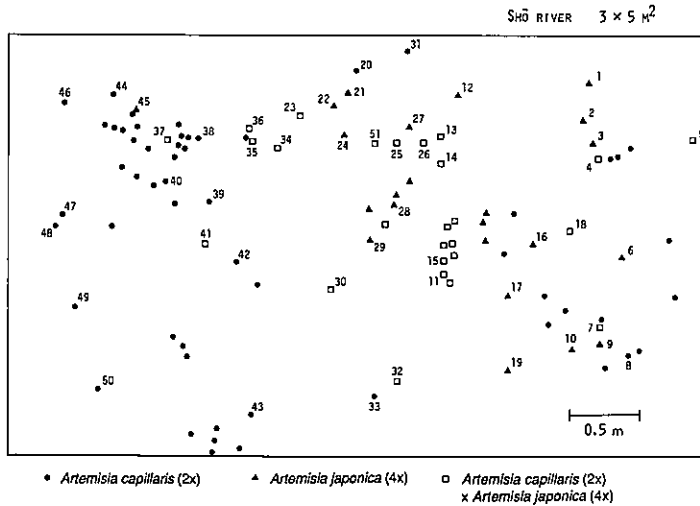


Fig. 3. The diagram illustrating the plot (3 × 5 m) where all *Artemisia* individuals were mapped and then collected for further detailed karyological and morphological studies. Filled circles indicate *A. capillaris* (2x); filled triangles *A. japonica* (4x); and open rectangles, hybrids between the above two species (3x). The final identification of all these individuals was based upon the chromosome counts.

as to the distributions of individuals of two *Artemisia* species, i. e., *A. capillaris* and *A. japonica*, and their putative hybrids (Fig. 3).

## 2. Gross Morphological Characters and Sources of Materials

The following 16 morphological, palynological and karyological characters were examined in the present study based on the mass collections made for typical *A. capillaris*, *A. japonica*, and their putative hybrids: (1) leaf shape; (2) leaf area/leaf (cm<sup>2</sup>); (3) leaf weight/leaf (mg/dry weight); (4) leaf area ratio (cm<sup>2</sup>/g dry weight); (5) seed length (mm); (6) seed width (mm); (7) external involucre length (mm); (8) internal involucre length (mm); (9) ratios of the internal/external involucre length; (10) floret numbers/head; (11) female floret numbers/total florets (%); (12) pollen fertility (%); (13) pollen size (μm); (14) chromosome numbers (2n); (15) karyotypes; and (16) meiotic behaviors of chromosomes.

The materials examined for gross morphological variations, pollen fertility, meiosis, somatic chromosome numbers, and karyotypes were mainly collected from the Sho River population (52 plants), but for comparison those from populations of *A. capillaris* from Iwasehama (12 plants) and Usaka (18 plants), Jinzu River, Toyama City, and of *A. japonica* from Usaka (20

plants), lower Jinzu River, Toyama City, Katakake (10 plants), upper Jinzu River, Nei-gun, and Nakada (10 plants), Sho River, Toyama Prefecture, where *A. capillaris* and *A. japonica* occur allopatric, were also examined.

## 3. Examinations of Pollen Size and Fertility, and Meiosis

Pollen size and fertility of 15 plants of *A. capillaris*, 17 of *A. japonica*, and 20 of putative hybrids from the Sho River population were examined (Table 1); in addition 30 plants of *A. capillaris* from Iwasehama and Usaka populations and 40 of *A. japonica* from Usaka, Nakada, and Katakake populations were also examined for comparison (Table 2).

Pollen grains were squeezed from anthers onto the slide glass and stained with 1% cotton blue, and then size and fertility were examined with an Olympus microscope.

For examinations of the meiotic behaviors of chromosomes, young flower buds were fixed with Newcomer's fixative (Newcomer 1953), stained with 1% acetic carmine, and observed with an Olympus microscope.

## 4. Somatic Chromosome Preparations

Somatic chromosome numbers and karyotypes were examined using the 8-hydroxyquinoline-

Table 1. Acmparation of various characters among *Artemisia capillaris*, *A. japonica* and their putative hybrids collected from Shogawa, Toyama

| Taxa   | Criteria N | Leaf area/leaf (cm <sup>2</sup> ) | Leaf weight/leaf (mg) | Leaf area ratio (cm <sup>2</sup> /g) | Seed Length (mm) | Seed width (mm) | External involucre length (mm) | Internal involucre length (mm) | Internal/External | Floret no./head | Femal fl./total fl. (%) | Pollen fertility (%) | Pollen diameter (μ) | Chr. no. (2n) |
|--|------------|-----------------------------------|-----------------------|--------------------------------------|------------------|-----------------|--------------------------------|--------------------------------|-------------------|-----------------|-------------------------|----------------------|---------------------|---------------|
| <i>A. capillaris</i>                         | 15         | 1.32<br>±0.77*                    | 13.23<br>±6.43        | 96.7<br>±22.8                        | 0.97<br>±0.09    | 0.49<br>±0.05   | 0.74<br>±0.10                  | 1.43<br>±0.17                  | 1.96<br>±0.272    | 8.13<br>±1.19   | 41.47<br>±8.08          | 79.99<br>±19.49      | 20.71<br>±1.51      | 18(2X)        |
| <i>A. capillaris</i><br>X <i>A. japonica</i> | 20         | 2.85<br>±1.50                     | 14.38<br>±7.39        | 200.5<br>±20.3                       | 0.86<br>±0.12    | 0.45<br>±0.05   | 0.90<br>±0.15                  | 1.43<br>±0.11                  | 1.644<br>±0.320   | 12.77<br>±2.14  | 65.49<br>±9.46          | 42.32<br>±18.70      | 22.89<br>±1.98      | 27(3X)        |
| <i>A. japonica</i>                           | 17         | 4.15<br>±1.23                     | 19.35<br>±5.49        | 219.0<br>±40.1                       | 0.94<br>±0.09    | 0.51<br>±0.03   | 1.08<br>±0.11                  | 1.68<br>±0.17                  | 1.558<br>±0.146   | 12.89<br>±2.29  | 65.48<br>±7.86          | 88.72<br>±6.94       | 24.33<br>±1.13      | 36(4X)        |

\*Mean ± S.D.

Table 2. Fertility of pollen grains of *Artemisia capillaris* (2X) and *A. japonica* (4X) from several populations in Toyama Prefecture

| Criteria<br>Taxa and<br>populations   | No. of plants<br>examined | Fertile<br>pollen | Sterile<br>pollen | Total<br>pollen<br>examined | %    |
|---------------------------------------|---------------------------|-------------------|-------------------|-----------------------------|------|
| <i>A. capillaris</i> (2X):            |                           |                   |                   |                             |      |
| Iwasehama,<br>Toyama City             | 12                        | 3009              | 3                 | 3011                        | 99.9 |
| Usaka, Jinzu<br>River, Toyama<br>City | 18                        | 5249              | 0                 | 5249                        | 100  |
| <i>A. japonica</i> (4X):              |                           |                   |                   |                             |      |
| Usaka, Jinzu<br>River, Toyama<br>City | 20                        | 5523              | 0                 | 5523                        | 100  |
| Nakada, Sho<br>River                  | 10                        | 3134              | 12                | 3146                        | 99.6 |
| Katakake,<br>Upper Jinzu<br>River     | 10                        | 2998              | 2                 | 3000                        | 99.9 |

acetic orcein squash method (Kawano and Itis 1963). Excised root tips in the native habitats were pretreated with 0.002 mol. aqueous 8-hydroxiquinoline at 17 °C for 4 hrs, then fixed with Farmer's solution for 1-2 min, stained in 1% aceto-orcein overnight, treated with a 1:1 mixture of 1% aceto-orcein and 1N HCl for ca. 15 min, and then squashed with a 1:9 mixture of glycerol and 45% glacial acetic acid aq. over the flame. The observations were made with an Olympus microscope. The total number of plants used in the karyological analysis was 62, including 20 plants of *A. capillaris*, 22 of *A. japonica*, and 20 of putative hybrids.

## Results

### 1. Population Structures and Underlying Environmental Regimes of *Artemisia capillaris* and *A. japonica* Habitats

*Artemisia capillaris* is a typical Compositae perennial of maritime sand dunes, often forming large but scattered populations, while *A. japonica* grows sporadically in somewhat sunny, small patchy tall grasslands developed on the river banks and at the margin of lowland deciduous forests, mainly consisting of *Quercus acutissima*, *Q. serrata*, *Q. variabilis*, *Carpinus laxiflora*, and *Alnus japonica*.

However, on the flood plain of large rivers, notably on the Japan Sea side of Honshu, we can often recognize that both species are growing side

by side, forming sympatric populations. In Toyama Prefecture, there occur many large rivers, such as the Kurobe, Katakai, Hayatsuki, Jyoganji, Jinzu, Sho and Oyabe Rivers; sympatric populations of both *Artemisia* species occur along all except for the Oyabe River. At the same time, typical sand dune populations of *A. capillaris* are developed along the sea coast facing the Toyama Bay. It is most likely that this typical sand dune perennial has migrated into the flood plains of these rivers from the river mouth and expanded its range further into the interior parts of the river flood plains, where these two closely related *Artemisia* species have met with and established sympatric populations. In this respect, these two species must have been originally allopatric.

A close examination of the habitats of these two *Artemisia* species clearly reveals that *A. capillaris* occurs on dry, sterile sand dunes (observed at Iwasehama, Hamakurosaki, in the suburbs of Toyama City) where only other typical sand dune species, such as *Lathyrus maritimus*, *Glehnia littoralis*, *Arabis stelleri* var. *japonica*, *Ischaemum anthephroides*, etc. grow, forming loose sporadic populations here and there on the dunes. Thus there is obviously no intensive interspecific competition. In contrast, *A. japonica* is a species of tall grasslands developed in the inland lowlands and foothills, often associated with *Lespedeza cuneata*, *Miscanthus sinensis*, *Solidago virgaurea* ssp. *asiatica*, etc., where occasional artificial or natural disturbances of the habitats may take place. The habitats of *A. japonica* may thus be defined as semi-natural grasslands exposed to occasional disturbances, where soil layers with humus develop to a certain extent. On the flood plains of the rivers, this species thus often occurs in drier humus-rich sites and also on the river bank, densely covered by several other shrubs and tall herbs.

Such an ecological situation is well illustrated in the belt-transect established on the flood plain of the Sho River in the present study (Fig. 2). Here, *A. capillaris* occurs on the gravelly sites in the center of the flood plain of the river, where no other tall herbs or shrubs occur except for the perennial herb *Anapharis margaritacea* var. *yedoensis*, which becomes more common in the

wetter sites near the stream. *Artemisia japonica*, however, occurs more abundantly near the river bank, associated with several other tall shrubs, vines, and herbs, such as *Rosa multiflora*, *Pueralia lobata*, *Lespedeza cuneata*, *Galium verum* var. *asiaticum*, etc. The sites where *A. japonica* is more abundant are characterized by humus-rich soils, a condition likewise well demonstrated by conspicuously lower C/N ratios of the soil samples analyzed (Fig. 2).

In the central part of the flood plain where both *Artemisia* species occur side by side, forming mixed populations, we could occasionally recognize peculiar intermediate *Artemisia* individuals in gross morphology. Judging from their various gross morphological characters, these plants are to be regarded as natural hybrids between *A. capillaris* and *A. japonica*. Indeed, there are numerous individuals showing such intermediate morphological features (Fig. 3). Upon examining the pollen fertility and somatic chromosome numbers, we could further firmly determine whether or not such intermediate forms in gross morphology are natural hybrids between the two *Artemisia* species growing side by side in the flood plain habitats.

## 2. Gross-Morphological Characteristics of *Artemisia capillaris*, *A. japonica*, and Their Putative F<sub>1</sub> Hybrids

*A. capillaris* (2x) is a perennial subshrub with somewhat woody stems, 30-100 cm in height, many branched, and silky-pubescent while young; sterile shoots have a tuft of rosulate leaves at the tip; upper leaves of the sterile shoots are long-petiolate, broadly clasping at the base, and bipinnatisect. The ultimate segments are filiform, 0.3-1 (-2) mm wide (Figs. 4-A, 5), and usually densely silky. Involucral bracts are 3- or 4-seriate; external involucre are very small, ovate, and obtuse ( $0.74 \pm 0.10$  mm in length), but internal involucre are much longer ( $1.43 \pm 0.74$  mm in length), elliptic, round at the apex, and keeled on the back. The ratios of internal/external involucre are  $1.960 \pm 0.272$ . Heads are very numerous, globose or ovoid, with about 8 florets (mean:  $8.13 \pm 1.19$ /head), of which ca. 40% are female flowers. Achenes are  $0.97 \pm 0.09$  mm (mean  $\pm$  S. D.) in length (Table 1).

*A. japonica* (4x), a perennial herb, is character-

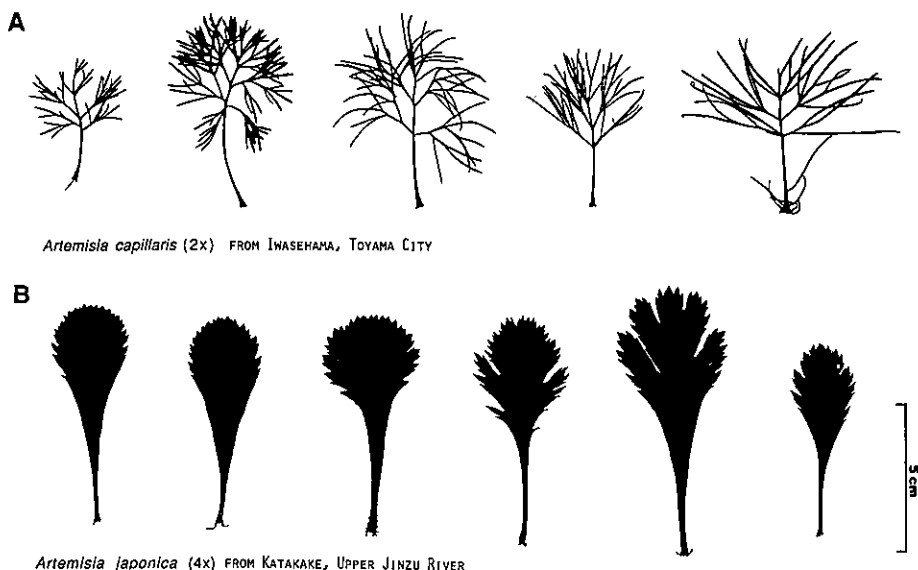


Fig. 4. Cauline leaves of typical *Artemisia capillaris* (2x) collected from the coastal sand dune habitat of Iwasehama, Toyama City, and those of *A. japonica* (4x) collected from Katakake, upper Jinzu River, Toyama Prefecture (see Fig. 1).

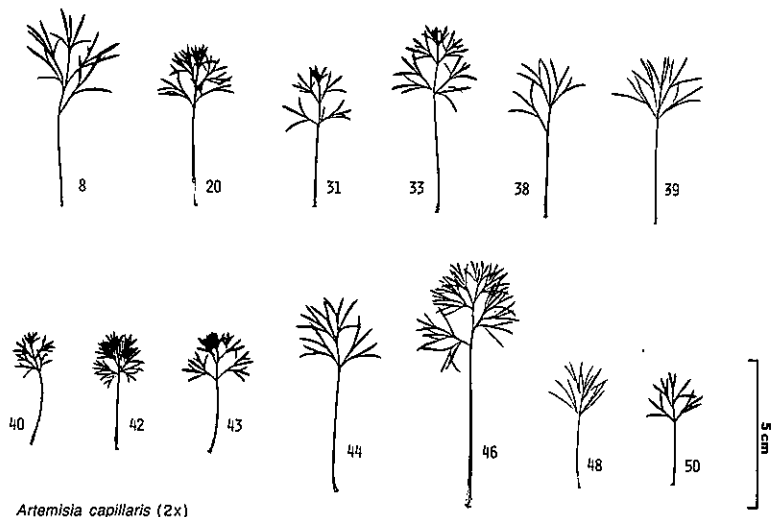


Fig. 5. Cauline leaves of *Artemisia capillaris* (2x) collected from the Sho River site. Each figure in the diagram corresponds to individuals mapped and shown in Fig. 3.

ized by having a tuft of leaves at the tip of the elongate non-flowering stems. Leaves of the sterile shoots are spatulate, 3.5-8 cm long, 1-3 cm wide, round, often pinnately lobed and toothed (Fig. 4-B), and loosely silky-pubescent on both sides; median leaves are rather fleshy, cuneate-spathulate, toothed, trifid, pinnately parted or pinnately divided (Fig. 6). Heads in panicles are small, many, ovoid-globose or ellipsoidal, slightly lustrous, yellow-green, and glabrous. External involucre are small, ovate, and obtuse (mean : 1.

08±0.11 mm in length); internal involucre are elliptic, round at the apex (mean : 1.68±0.17 mm in length). The ratios of internal/external involucre are 1.56±0.15. The number of florets/head is 12.89, of which female florets are 65.48±7.86%. Thus, the proportion of female florets is somewhat higher in *A. japonica*. Achenes are 0.94±0.09mm (mean±S. D.) in length.

The plants which possessed somewhat intermediate leaf characters (Fig. 7) are considered to be putative hybrids (and indeed all selected interme-



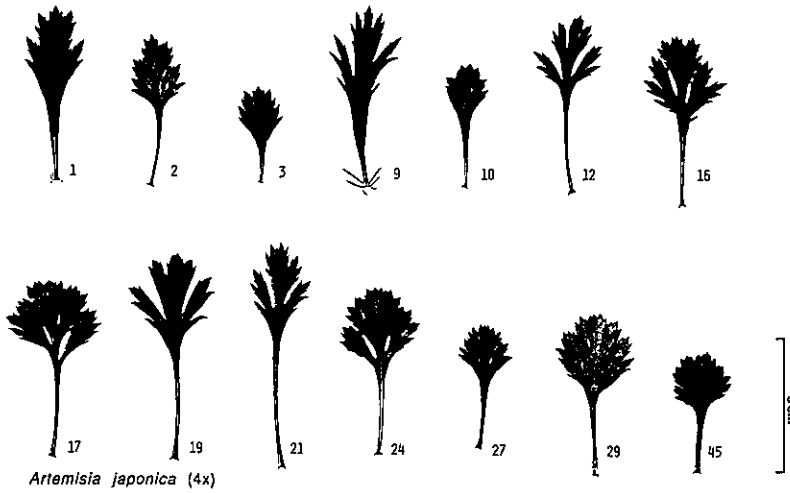


Fig. 6. Culine leaves of *Artemisia japonica* (4x) collected from the Sho River site. Figures in the diagram correspond to those mapped and shown in Fig. 3.

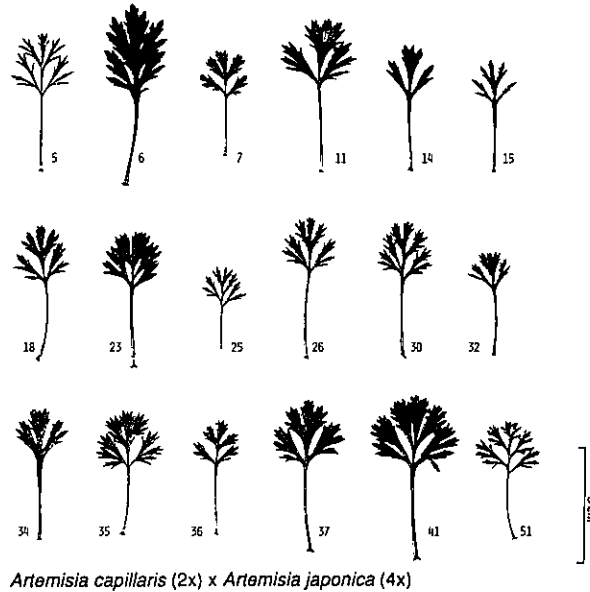


Fig. 7. Culine leaves of hybrid *Artemisia* individuals (3x) between *A. capillaris* (2x) and *A. japonica* (4x). Each figure corresponds to those which were mapped and shown in Fig. 3.

diat plants karyologically examined turned out to be 3x and thus assumed to be natural hybrids). Leaves of the sterile shoots are more or less spatulate, but leaf segments are diverse in tooth size or in serration, as well as in leaf area ratio (cm<sup>2</sup>/g) (Fig. 8) and leaf weight/leaf (Table 1). The length of both the external and internal involucre was intermediate between *A. capillaris* and *A. japonica* (Table 1). The number of florets per head and the proportion of female florets were much closer to *A. japonica*, showing more or

less the same values (see Table 1).

### 3. Somatic Chromosome Numbers and Karyotypes

*A. capillaris* has been known to be diploid with 2n=18 somatic chromosomes (Shimotomai 1947; Arano 1962, 1965; Masumori 1961; Masumori et al. 1973; Masumori 1976b), and the same chromosome number was confirmed in the typical forms of *A. capillaris* collected from the Iwasehama and Sho River populations. The karyotype of *A. capil-*

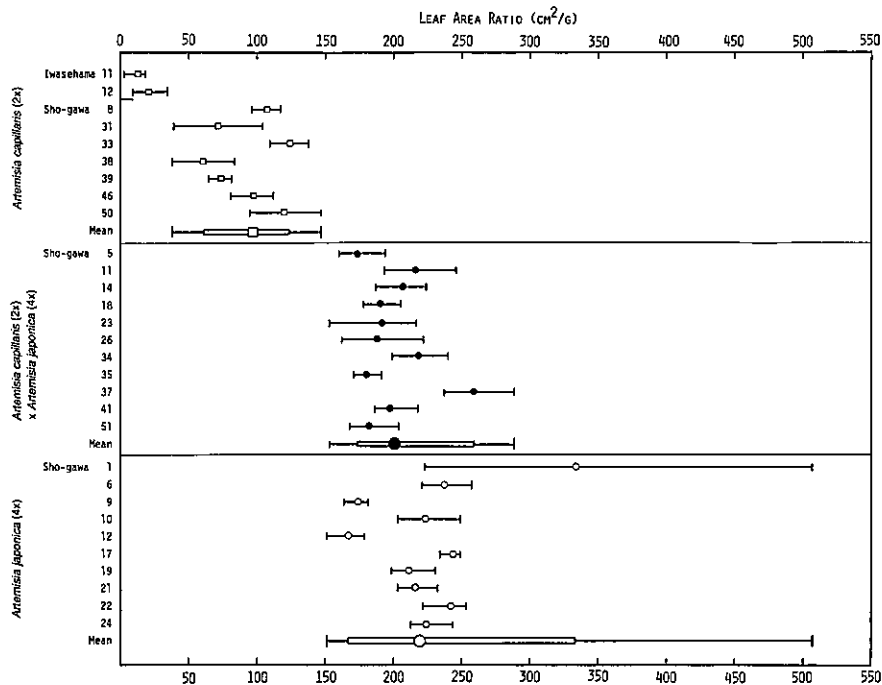


Fig. 8. Leaf area ratio ( $\text{cm}^2/\text{g}$ ) of *Artemisia* individuals collected from the Sho River site. For each individual, means, maximum and minimum values are shown, and then means, maximum values and minimum values, and standard deviations for *A. capillaris*, *A. japonica*, and their hybrids are exhibited. Figures in the diagram correspond to those mapped and illustrated in Fig. 3. The measurements taken from two typical *A. capillaris* plants collected from Iwasehama, Toyama City, are also shown for comparison.

*laris* is composed of two large submedian pairs with a satellite on the abaxial end of the short arms, one large subterminal pair, and six median or submedian medium pairs (Figs. 9A, C and 11). The number of satellites, however, varied from one to four in the plants examined.

On the other hand, *A. japonica* has been known to be tetraploid with  $2n=36$  somatic chromosomes (Shimotomai 1947; Suzuka 1950, 1952; Arano 1962). The same chromosome number was also counted in the typical forms of *A. japonica* that occurred in the Katakake, upper Jinzu River and Sho River populations. The karyotype of *A. japonica* consists of two large median pairs occasionally with a satellite on the abaxial end of the short arms (often satellites were invisible, however, and its presence was not confirmed in all preparations), eight pairs of large median or submedian chromosomes in constriction, two pairs of large subterminal pairs, often with a satellite on the abaxial end of the short arms, two pairs of terminal chromosomes, and four small pairs of

median or submedian chromosomes (Figs. 10 and 11).

All 27 individuals intermediate in gross morphology that were karyologically examined in the present study proved to be triploid with  $2n=27$  somatic chromosomes (*cf.* Table 1). This fact clearly indicates that such morphologically intermediate forms are  $F_1$  hybrids. The karyotypes of triploid plants are rather variable, having unequal numbers of satellite pairs and variable chromosomal pairs, which is a good indication of obvious hybridization (Figs. 9B, D and 11). However, exact identity of each chromosome sets, *i. e.*, its origins from diploids or tetraploids etc., was not determined in all cases, since most of the chromosome complements are consisting of median or submedian chromosomes of more or less similar sizes at metaphase in somatic cell division. In the root-tip cells pretreated with 8-hydroxyquinoline or colchicine, the degree of chromosome condensation at metaphase is so great that often we can not identify exactly the

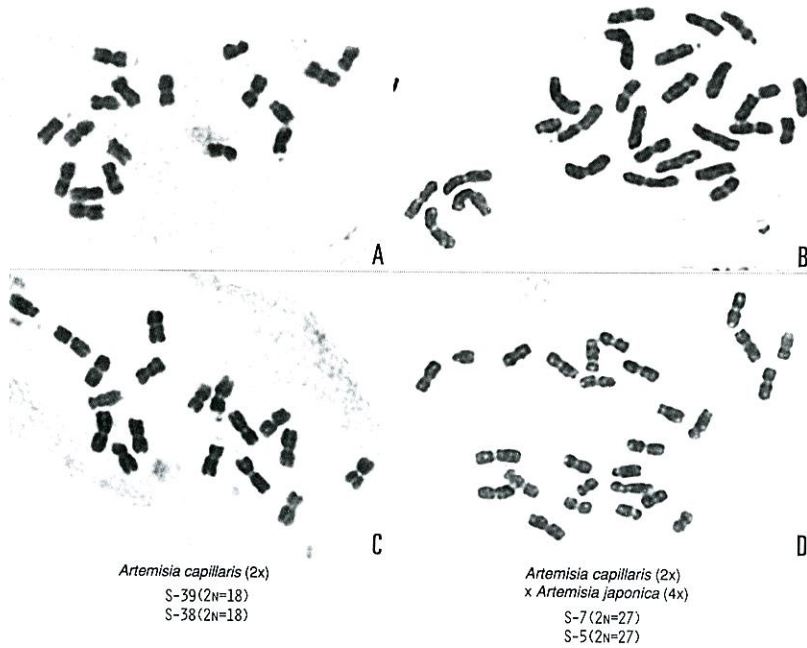


Fig. 9. A and C, photomicrographs illustrating somatic chromosome complements of *Artemisia capillaris* ( $2n=18$ ); B and D, those of triploid hybrids ( $2n=27$ ) between *A. capillaris* and *A. japonica*. Materials were collected from the Sho River site, and karyologically examined.



Fig. 10. A and B, photomicrographs illustrating somatic chromosome complements of *Artemisia japonica* ( $2n=36$ ). Materials examined are from the Sho River site.

homologues in the cell plates.

#### 4. Chromosome Pairings in Meiosis

Meiotic chromosome pairings were also examined on ten selected triploid plants (Nos. 5, 11, 14, 18, 25, 26, 34, 35, 37, and 41 in Fig. 3).

As shown in Fig. 12, the pairings were all irregular, forming two to four univalents, three to four trivalents, and five to six bivalents. In contrast, both diploid *A. capillaris* ( $2n=18$ ) and tetraploid *A. japonica* ( $2n=36$ ) examined all exhibited 9 and 18 regular bivalents, respectively.

### 5. Pollen Size and Fertility

Pollen size and fertility were examined in both mother plants and their putative hybrids in the Sho River population (Fig. 13). As expected, diploid *A. capillaris* possessed the smallest pollen in size, ranging from 17 to 26  $\mu\text{m}$  (mean: 20.71  $\mu\text{m} \pm 1.51$ ), and its fertility rate was ca. 80% (Table 1); whereas tetraploid *A. japonica* had the largest pollen, 20.5-31  $\mu\text{m}$  in size (mean: 24.33  $\mu\text{m} \pm 1.33$ ), with a high fertility rate of ca. 89% (Table 1, Fig. 14).

In contrast, pollen grains of triploid plants were quite variable in size, ranging from 15 to 32.5  $\mu\text{m}$  with exceedingly variable pollen fertility (mean: 42.32  $\pm 18.70\%$ ) (see also Figs. 14, 15 and 16) This is also a good indication of hybridization of these intermediate forms.

Figure 15 demonstrates pollen fertility (%) of selected individuals of *A. capillaris* (2x) (Nos. 8, 31, 33, 38, 39, 46 and 50), *A. japonica* (4x) (Nos. 1, 6, 9, 10, 12, 17, 19, 22, and 24), and hybrids (3x) (Nos. 5, 11, 14, 18, 25, 26, 34, 35, 37, 41 and 51) collected from the Sho River site (all mapped individuals in Fig. 3). The pollen fertility (%) of *A. capillaris* plants collected from the coastal sand dune habitat of Iwasehama, Toyama City, and the flood plain habitat of Usaka, Jinzu River; and also those of *A. japonica* from the flood plain habitats of Katakake, upper Jinzu River, Usaka, lower Jinzu River, and Nakada, Sho River were also included for comparison (Table 2).

As expected, pollen grains of all triploid plants from the Sho River population were exceedingly variable in size, mostly completely lacking nuclei, but several diploid and tetraploid plants referable to *A. capillaris* and *A. japonica* from the Sho River site also showed unexpectedly low pollen fertility, lacking nuclei, which may be due to the effects of partial gene flow from triploid plants by backcrosses with parental plants. On the other hand, all the plants of *A. capillaris* and *A. japonica* from some other allopatric populations

examined for comparison, pollen fertility was nearly 100 % (Table 2).

### 6. Character Correlations in Parental Species and Hybrids

Character correlations were examined more critically in both *A. capillaris* and *A. japonica* and their hybrids. Figure 16 illustrates the character correlations by a pictorialized scatter diagram for diploid *A. capillaris*, tetraploid *A. japonica*, and their triploid hybrids or hybrid derivatives. It is very clear that most of the triploid plants exhibit more or less intermediate features, but a few triploid individuals fall into the variation range of *A. japonica*, especially in leaf characters, despite the fact that they have very low pollen fertility.

We have also examined the variabilities of the two parental *Artemisia* species and their hybrids by principal component analysis (Figs. 17 and 18). The percentages of total variance were 36.09% in the first component ( $Z_1$ ), 20.03 in the second component ( $Z_2$ ), and 12.50 in the third component ( $Z_3$ ). The first two components ( $Z_1$  and  $Z_2$ ) extracted from the correlation matrix accounted for 56.1% of the total variance (Table 3). Considering the factor loading of 13 characters, the first principal component ( $Z_1$ ) seems to indicate various size characters such as leaf area and weight, involucre lengths, floret numbers and pollen diameters, whereas the second principal component ( $Z_2$ ) reveals variations in pollen fertility (Fig. 17).

The results of the PCA (Fig. 18) revealed that individuals of *A. japonica* (4x) are in the first quadrant and those of *A. capillaris* (2x) are in the second quadrant, whereas those of hybrids (3x) are all in the third and fourth quadrants. It is interesting to note that some diploid and tetraploid individuals also fall in the range of hybrids, suggesting a possible partial gene flow from triploid plants to *A. capillaris* and also to *A. japonica* individuals by heterogamy. However, since the number of individuals examined in the present analysis is rather limited, further studies may be needed in order to confirm as to the occurrence of heterogamy.

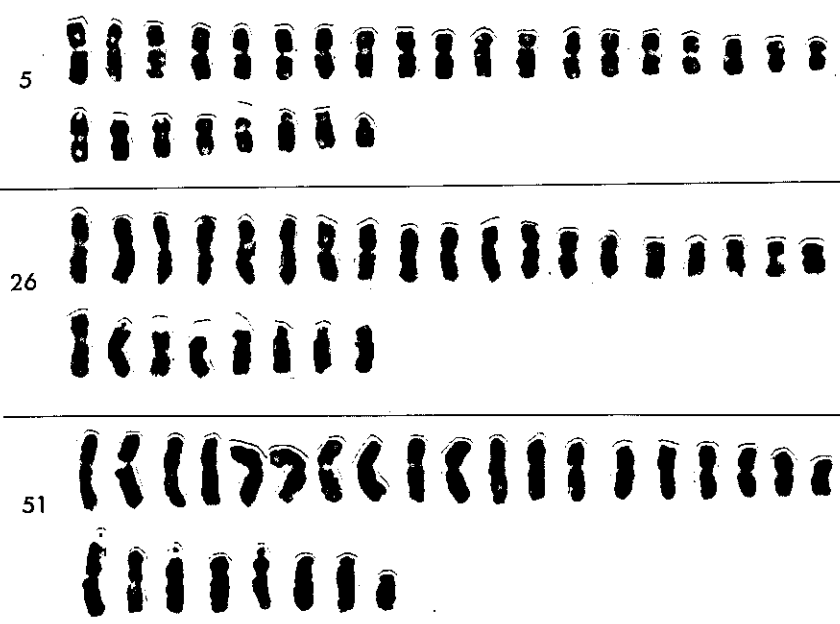
### Discussion

The results of the present study clearly demonstrate that the *Artemisia* plants intermediate in

*Artemisia capillaris* (2x)



*Artemisia capillaris* (2x) x *Artemisia japonica* (4x)



*Artemisia japonica* (4x)



Fig. 11. Somatic chromosome complements of *Artemisia capillaris* ( $2n=18-2x$ ), *A. capillaris* x *A. japonica* ( $2n=27-3x$ ), and *A. japonica* ( $2n=36-4x$ ). Figures (38 and 39: *A. capillaris*; 5, 26, and 51: hybrids; 3 and 19: *A. japonica*) correspond to those mapped and collected from the Sho River site, shown in Fig. 3.

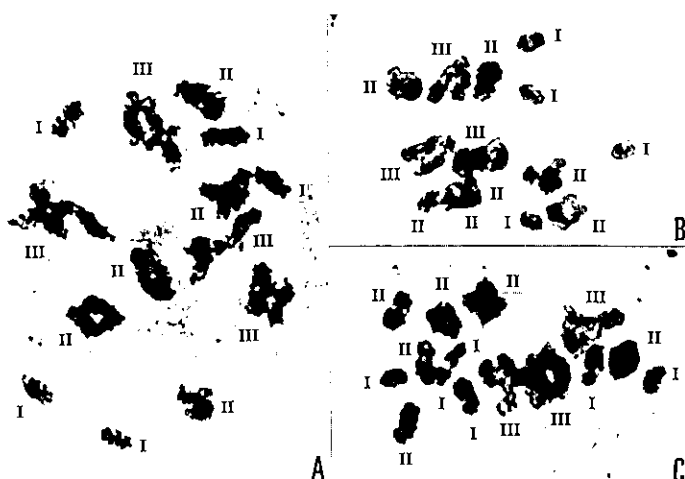


Fig. 12. A, B, and C: Photomicrographs illustrating meiotic behaviours of triploid hybrids ( $2n=27$ ) between *A. capillaris* ( $2n=18$ ) and *A. japonica* ( $2n=36$ ). Note that three to four univalents, two to three trivalents, and four to six bivalents occur, which indicates the degree of heterogeneity in the genomic constitution between these two diploid and tetraploid *Artemisia* species.

their gross morphological characters, which are occasionally found in the sympatric populations of diploid *A. capillaris* and tetraploid *A. japonica* developed in the flood plain habitats of the Sho River, Toyama Prefecture, central Honshu, all proved to be  $F_1$  hybrids or hybrid derivatives (with  $2n=27$  somatic chromosomes) originated from the hybridization between these two *Artemisia* taxa. This is in agreement with Masumori's previous karyological findings (Masumori 1976b).

Somewhat similar ecological situations occurred in the flood plain habitats of other large rivers in Toyama Prefecture, e. g., the Jinzu, Jyoganji, Kurobe Rivers and so on, where both *Artemisia* species form sympatric populations; as expected, we also found there similar putative hybrids between *A. capillaris* and *A. japonica*, showing intermediate morphological features (cf. Table 1). The background ecological conditions of all these flood plain habitats are more or less the same, with irregular natural and artificial disturbances

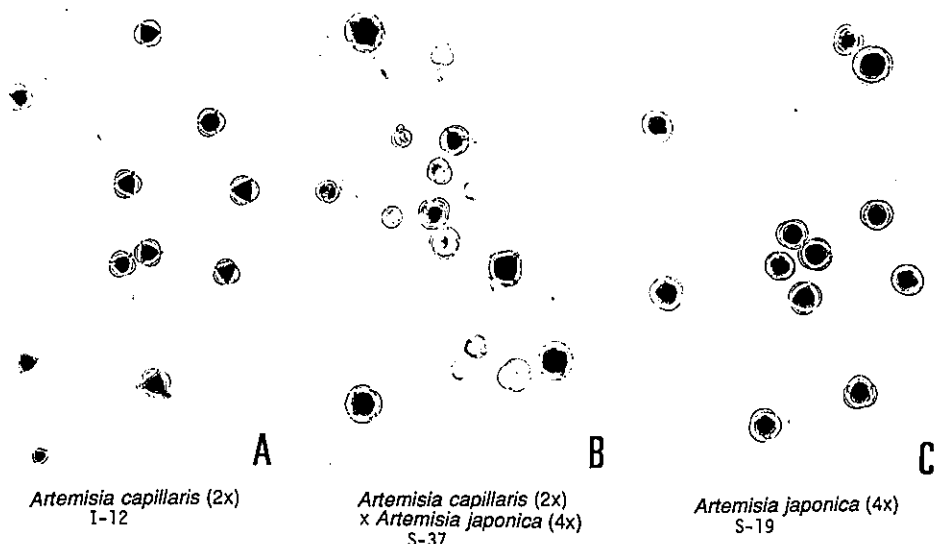


Fig. 13. Photomicrographs showing pollen grains stained with 1% cotton blue of *Artemisia capillaris* (2x) (I-12 from Iwasehama, Toyama City), *A. japonica* (4x) (S-19 from the Sho River site), and hybrids (3x) (S-37 from the Sho River site) between them. Note unstained, irregular-sized pollen grains of triploid plants, occasionally lacking nuclei.

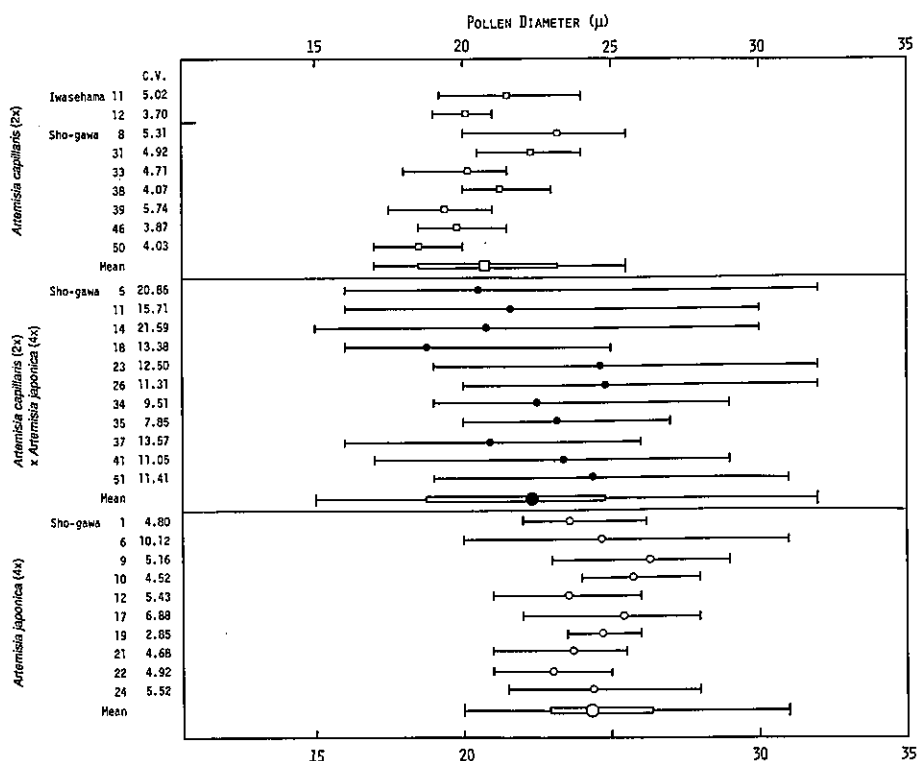


Fig. 14. The diagram illustrating the size variations of pollen grains of *Artemisia capillaris* (2x), *A. japonica* (4x), and their hybrids (3x). For each individual of these *Artemisia* plants examined, means, maximum and minimum values, and C. V. are shown, and further means, maximum and minimum values, and S. D. are shown for pooled samples. Figures in the diagram correspond to the plants mapped and collected from the Sho River site shown in Fig. 3. For *A. capillaris*, two selected plants collected from Iwasehana, Toyama City, are also included for comparison.

here and there, often accompanied by flooding and artificial fires (Fig. 19).

Species of the genus *Artemisia* are all known to be wind-pollinated, and thus if sympatric populations are once formed and there is no strong sterility barrier or reproductive isolation between the two taxa, hybridization may easily take place. Indeed, in the present study, all clearly intermediate *Artemisia* plants in gross morphological characters turned out to be triploid F<sub>1</sub> progeny or derivatives with 2n=27 chromosomes, with variously changing levels of pollen fertility. This fact suggests that hybridization occurs in such sympatric populations of these two *Artemisia* species, recruiting new hybrid progenies in the populations more or less continuously. Otherwise, all these triploid hybrids will soon be eliminated from the populations (Fig. 17). However, judging from exceedingly low pollen fertilities and somewhat intermediate leaf characters of some tetraploid plants (Figs. 3, 5, 6, 7 and 15), we cannot

deny the possibility of hybrid derivatives produced by partial gene flow, i. e., heterogamy, from triploids to diploid or especially to tetraploid plants. Indeed, some of the tetraploid plants (e. g., Nos. 12, 19, and 21 in Fig. 6), though referred to *A. japonica* based on floral characters, were not always typical in their leaf characters as found in coastal or inland allopatric populations (Fig. 4-A and B) and thus at a glance indistinguishable from triploid hybrid plants, unless the chromosome number was determined.

The occurrence of natural hybrid swarms in plants is of course a universally known phenomenon (Stebbins 1950, 1971; Anderson 1949; Grant 1963, 1981, 1985), and various classic examples—including so-called introgressive hybridization or introgression (Anderson and Hubricht 1938; Anderson 1949; Riley 1938, 1939; Kawano 1961; Kawano and Noguchi 1973)—have been reported from numerous plant groups. Above all, natural interspecific hybridization and subsequent poly-

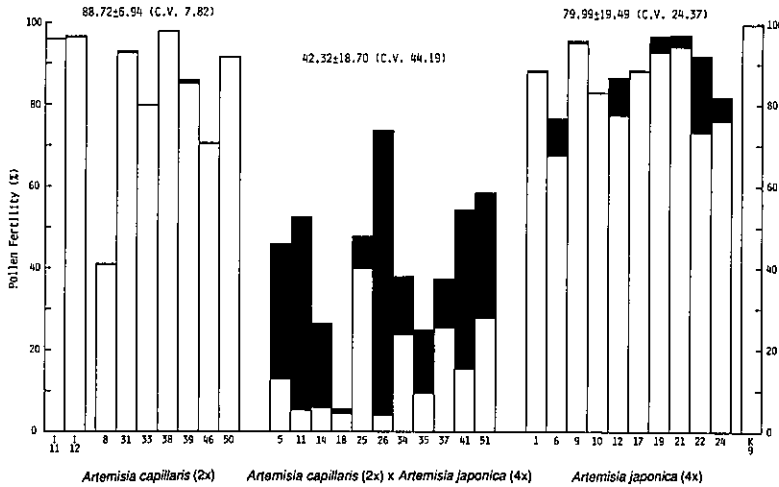


Fig. 15. Pollen fertility of *Artemisia capillaris* (2x), *A. japonica* (4x), and their hybrids (3x). Each figure in the diagram corresponds to the plants mapped and collected from the Sho River site shown in Fig. 3. I-11 and I-12 are those which were collected from Iwasehama, Toyama City, and K-9 is from Katakake, upper Jinzu River, Toyama Prefecture, which are included here for comparison. The black part of the diagram indicates proportions of pollen grains lacking nuclei.

ploidization are known to be unique but frequent in plants, and have no doubt played significant roles in the process of speciations, e.g., *Aegilops* and *Triticum* (Kihara and Nishiyama 1930; Kihara 1954, 1957; Zohary and Feldman 1962; Johnson 1967a, b, 1968, 1972a, b; Johnson et al. 1967; Johnson and Hall 1965; Hall et al. 1966; Nakai and Tsunewaki 1971), *Trillium* (Kurabayashi, 1958; Samejima and Samejima 1962), *Asplenium* (Wagner 1954; Smith and Levin 1963), *Tragopogon* (Ownbey 1950; Ownbey and McCollum 1953) and *Cardamine* (Urbanska and Landolt 1978; Urbanska 1977a, 1977b, 1978, 1980, 1981, 1984). However, taxonomists have likewise recorded a large number of putative interspecific hybrids from various plant groups in floras of different regions (e.g., Stebbins 1950, 1971; Fernald 1950; Munz and Keck 1965; Kitamura et al. 1960; Kitamura and Murata 1961; Kitamura et al. 1967; Stace 1975).

All these facts clearly indicate the common occurrence of interspecific hybridization in natural populations of plants. However, the roles of hybridization in terms of speciation seem to be not very clear in all circumstances, especially in the cases of hybrids produced between plants with different ploidy levels, e.g., between 2x and 4x, just as shown in the present study. Normally, triploids are sterile and do not produce fertile F<sub>2</sub>

progeny, unless chromosome doubling occurs simultaneously or some other mechanisms such as agamospermy or vegetative reproduction are involved for the recruitment of hybrid progeny. The case history known in *Cardamine* × *insueta* (2n=24), which possibly originated in hybridization between unreduced gametes of *C. rivularis* (2n=16) and *C. amara* (2n=16), is an extraordinary example. It was assumed that some triploid plants produced a small amount of viable pollen, and the limited reproduction by seeds resulted in a most unusual pattern of heterogamy (Urbanska and Landolt 1978; Urbanska 1987).

The examples shown in *Aegilops-Triticum* (Kihara 1954; Zohary and Feldman 1962), *Trillium* (Kurabayashi 1958; Samejima and Samejima 1962), *Cardamine* (Urbanska 1977b, 1980, 1984) and *Asplenium* (Wagner 1954; Smith and Levin 1963) are all cases in which subsequent polyploidization (i.e., amphiploidy) played a most significant role for the differentiation of these particular plant groups.

Normally, segregation in the F<sub>1</sub> or any subsequent generations derived from an interspecific cross can be completely stopped or greatly restricted by various mechanisms. The occurrence of peculiar intermediate forms of *Artemisia* individuals in sympatric populations developed in the flood plain habitats of the Sho River, Toyama



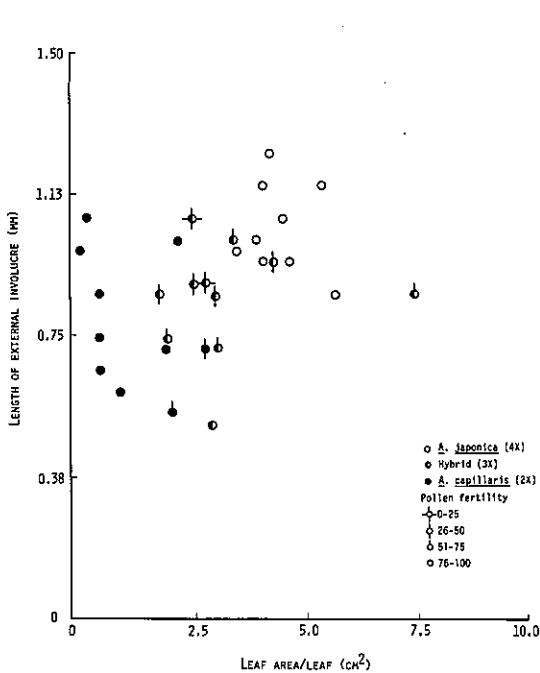


Fig. 16. Scatter diagram illustrating character correlation between leaf area/leaf ( $\text{cm}^2$ ) and length of external involucre (mm) of *Artemisia capillaris* (2x), *A. japonica* (4x), and their hybrids (3x), together representing pollen fertility data. Most of the triploid hybrids showed intermediate features between the parental species, but note that some triploid hybrids fall in the variation range of the *A. japonica* leaf size.

Prefecture, e.g., Nos. 12, 16, 19, and 21 (Fig. 6; also see Figs. 7 and 16), however, suggests that partial gene flow from diploid *A. capillaris* or triploid hybrids into tetraploid *A. japonica* may be taking place, and due to heterogamy some heterogenous individuals in genome constitution may have been produced, with  $2n=36$ , a tetraploid somatic chromosome number. Interestingly, these peculiar forms of tetraploid plants with hybrid-like leaf characters showed considerably low pollen fertility, lacking nuclei, a feature commonly noted in the triploid plants (see Fig. 15). In order to confirm, however, whether or not what is the true situation, we need to examine more ample individual plants in such sympatric populations.

Grant (1981) summarized various previously known mechanisms of hybrid stabilization as follows; (1) vegetative propagation, (2) agamo-

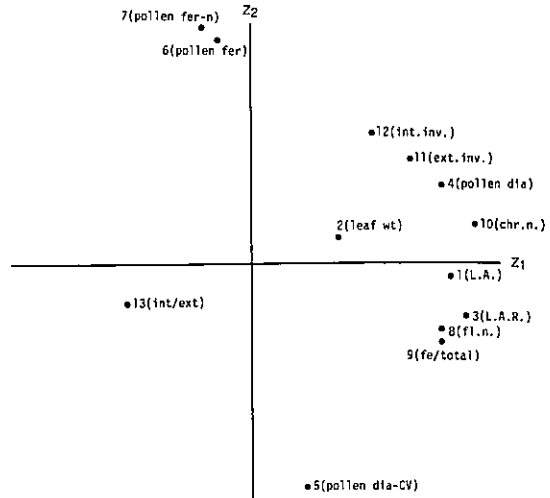


Fig. 17. Principal component analysis of various morphological, pollen, and chromosome characters of *Artemisia capillaris* (2x), *A. japonica* (4x), and their hybrids (3x) collected from the Sho River population. 1 (L. A.), leaf area/leaf ( $\text{cm}^2$ ); 2 (leaf wt), leaf weight/leaf (mg dry weight); 3 (L. A. R.), leaf area ratio ( $\text{cm}^2/\text{g}$  dry weight); 4 (pollen dia), pollen diameter ( $\mu\text{m}$ ); 5 (pollen dia-CV), coefficients of variations of pollen diameter; 6 (pollen fer), pollen fertility(%); 7 (pollen fer-n), pollen fertility(% of sample plants from Iwasehama, Toyama City (*A. capillaris*) and Katakake, upper Jinzu River (*A. japonica*)); 8 (fl. n.), floret number/head; 9 (fe/total), female floret/total floret(%); 10 (chr. n.), somatic chromosome numbers (2n); 11 (ext. inv.), external involucre length (mm); 12 (int. inv.), internal involucre length (mm); 13 (int/ext), internal involucre length: external involucre length ratio.

spermy, (3) permanent translocation heterozygosity, (4) permanent odd polyploidy, (5) amphiploidy, (6) recombinational speciation, and (7) the segregation of a new type isolated by external barriers. However, in the case of *Artemisia* hybrids reported in the present paper, the breakdown of hybrid swarms appears to be repeatedly occurring, and thus the current status of hybrid swarms is more or less similar to those reported from *Cardamine*  $\times$  *insueta* (Urbanska 1987).

Hybrid swarms like those found in *Artemisia*, however, may be rather common in the sympatric populations consisting of 2x and 4x species, where no sterility barrier or specific isolation mechanisms exist. On the other hand, the elimination (or selection) of such triploid individuals from the populations may be taking place simultaneously

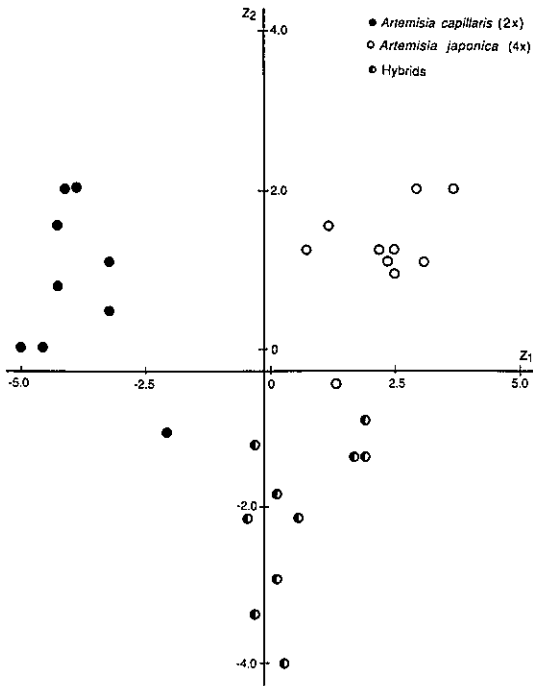


Fig. 18. Results of principal component analysis based on 13 characters (as shown in Fig. 17) of *Artemisia capillaris* (2x), *A. japonica* (4x) and their triploid hybrids projected on the  $Z_1$ - $Z_2$  axis.

in changing environments, such as in the flood plains of rivers exposed to frequent strong natural or artificial disturbances. Considering all the cases hitherto reported, the expansion of their ranges or habitats, or introduction into alien territories, first provide opportunities for the two or more closely related species which were once allopatric, and thus ecological or at least spatial isolation existed previously, to become contiguous or overlapping in their ranges, and then to give further chances for mating or hybridization (Ownbey 1950; Ownbey and McCollum 1953).

In short, the establishment and survival of the first hybrid generation is the necessary prerequisite for further evolutionary development. However, subsequent hybrid generations may require further site differentiation for successful establishment (Urbanska 1987). The vast majority of the present open and "hybridized" habitats are the result of human intervention; many are dependent upon regular management if they are not to disappear. This management usually involves manipulation of the moisture content or nutrient

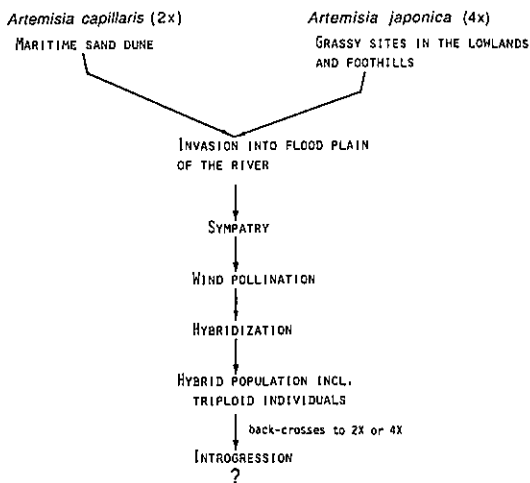
content of the soil resulting in changes in the vegetation cover (Urbanska 1987). The hybrid swarms in such a sympatric population of two closely related species may thus be maintained temporarily in such somewhat unstable, changing environments exposed to occasional human or natural disturbances, also with a continuous supply or recruitment of hybrid  $F_1$  progeny ( $3\times$ ) by hybridization between diploid and tetraploid plants within a sympatric population, with a limited extent of gene flow into diploid or tetraploid parental individuals by backcrosses.

The density of individuals within a sympatric site and the roles of pollination mechanisms, thus, seem also to be very significant for the formation of interspecific hybrids, especially for wind-pollinating plants such as *Artemisia* species. Also, seasonal (or allochronic), ethological, or mechanical isolations may play key roles for maintaining these different species populations separately as independent reproductive communities even if there are no internal reproductive isolating barriers differentiated—*i.e.*, in another word, no postfertilization (prezygotic as well as postzygotic) isolating mechanisms existing between the two species. The situations found in sympatric *Artemisia* populations here are somewhat different from those of interspecific hybrid populations of diploid species, where often introgression—*i.e.*, more frequent back-crosses to either one of parental species individuals are taking place (Anderson 1949; Kawano 1961; Kawano and Noguchi 1973), or development of some other specific reproductive systems, *e.g.*, agamospermy or vegetative propagation (Stebbins 1950; Grant 1981), and cleistogamy (Watanabe *et al.* 1992) is involved for the maintenance of hybrid swarms. However, judging from the variabilities of various gross morphological characters, pollen fertility, and chromosome numbers (Figs. 6, 7, and 15), we cannot deny the possibility that frequent reciprocal outcrossings are taking place among diploid, triploid, and tetraploid individuals in such a sympatric population, although these abnormal offspring produced temporarily may be exterminated rather quickly from the population.

Natural hybrid swarms, just as found in sympatric populations of two diploid and tetraploid *Artemisia* species demonstrated in the pres-

Table 3. Eigenvalues, contributions (%), and accumulated contributions(%) for principal components

| Components                  | I     | II    | III   | IV    |
|-----------------------------|-------|-------|-------|-------|
| Eigenvalue                  | 6.135 | 3.405 | 2.125 | 1.455 |
| Contribution(%)             | 36.09 | 20.03 | 12.50 | 8.557 |
| Accumulated contribution(%) | 36.09 | 56.12 | 68.62 | 77.18 |

Fig. 19. The process of the formation of hybrid swarms in two *Artemisia* species, *A. capillaris* (2x) and *A. japonica* (4x).

ent study, may represent a sort of deadlock situation in terms of evolutionary processes occurring in wild sympatric populations of two closely related species, unless further simultaneous polyploidization or differentiations of some other mechanisms, including agamospermy, vegetative propagation, and so forth (Grant 1981) take place there. Perhaps, however, such circumstances would not be very rare in the natural populations, representing the initial stages of differentiation through hybridization in plants, just as found in the hybrid populations of *Trillium* or *Cardamine* species (Kurabayashi 1958; Samejima and Samejima 1962; Urbanska 1987). Concerning the fate of such hybrid populations, field observations seem to be worth continuing; the results obtained will shed a light on the differentiation process of plant populations.

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### 摘 要

富山県には北アルプス立山山系、白木峰、金剛堂山、大倉山を源流とする黒部川、片貝川、常願寺川、神通川、早月川、庄川、小矢部川の7大河川が存在するが、小矢部川を除く6つの河川にはアキノキリンソウ、カワラハハコ、カワラヨモギなど、氾濫源に特徴的な多年草の植物群落が発達する。しかしながら、カワラヨモギは、元来海岸砂丘のやや不安定な環境にその主な生育地をもつ種で、これらの大河川の下流域に発達する集団は、海岸砂丘より長年に渡る移住の結果成立し、形成されたものとみなされる。

近年、これらの河川の氾濫源は下流に近い地域ほど大規模な開発行為のためにその原型を失いつつある。しかし、一部の地域ではまだ若干なりともその本来の環境を保持し、カワラヨモギの集団が残存しており、そこに丘陵地帯の落葉樹林内や林縁に多い同じヨモギ属 *Capillaris* 節のオトコヨモギが侵入し、カワラヨモギと同所的集団を形成する。著者らは、10数年前より、これらの同所的集団の中に、外部形態、特に葉の形質から一見してカワラヨモギとオトコヨモギの中間型が多数混生することに注目してきた。これらの中間型を示す植物は明らかに、これら両種の種間雑種とみなされるが、本研究では、庄川の氾濫源に発達する一集団を選び、外部形態諸形質、体細胞染色体数、核型、減数分裂時の染色体の対合、花粉のサイズと稔性(Cotton-blueによる染色率)などに関して詳細に比較研究し、併せて主成分分析を行うなどして、これらヨモギ属2種の同所的集団の構成個体の示す変異性に関して解析を行うと同時に、それらの起源についても考察を行った。

その結果、中間型のほとんどの個体が  $2n=27$  の3倍体で、2倍体のカワラヨモギ ( $2n=18$ ) と4倍体 ( $2n=36$ ) のオトコヨモギの  $F_1$  雑種であることが判明した。この事実は、3倍体の核型構成、減数分裂時の染色体の対合異常、花粉サイズの幅広い変異や、その著しく低い稔性などからも確かめることが出来た。しかしながら、4倍体、2倍体植物の中にも、葉の形質からみてこれらの母種の正常な変異域より著しくはみだし、しかも極めて低い花粉稔性しか示さない個体が混在することが確かめられた。これらの個体の正確な正体はまだ不明であるが、同所

的集団内で形成された  $F_1$  雑種の異型配偶子と母植物との戻し交雑の結果形成された部分的なヘテロのゲノム構成を持つ4倍体、あるいは2倍体個体である可能性もある。いずれにせよ、大半の雑種性3倍体は不稔で種子形成は正常には行われないので、母

種個体間で繰り返し交雑が行われることによって集団内に引き続き生み出されているものと推定される。

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○井波一雄：西原禮之助さんを想う Kazuo Inami: Obituary of the late Mr. Reinosuke Nishihara

敢えてこの先人を西原さんと呼ぶほどに親しく懐かしい植物の友でありました。

氏が岡山きっての銘酒「お多美鶴」の社長さんであることを存じ上げるず一つと以前から氏のご令名は存じ上げ各種学会が各地で全国集會をもたれた折々には、よくご同席の榮をいただいて自社の製品詰めの小瓶などを全員に用意されたご温情を飲めないながらいつも有難く、ヤアヤアと親しげにご挨拶を交したことなどが思い出されます。

昭和5年から植物に関心を持ち採集に力をいれつづけて県下各地はもとよりひろく全国各地を採集して歩かれたご様子は氏のご著作「岡山の植物」(昭和39年刊。岡山文庫1)によくまとめられて巻頭自序にも「素人の私共(生態写真を倉敷レーヨンの岡山工場の古谷野 寛氏が提供された)がこのように本としてまとめることができたのも、故牧野富太郎博士、故小泉源一博士、前川文夫博士、北村四郎博士等の諸先生のご指導とご激励の賜物と深く感謝致します云々」と述べられた通りであります。

同書にオオバイカイカリソウを掲げられた解説に「本種は阿哲、川上および備後の北部、主として石灰岩露出地帯を中心として極めて狭い範囲に限られている」と地元岡山県での観察を明記され、さらにオオバイカイカリソウとトキワイカリソウとの天然交雑にも触れ、前川文夫博士のスズフレイカリソウ、小泉源一博士のウメザキイカリソウなど諸説に千変万化の微妙な差を観察されて「どれがトキワイカリソウでどれがオオバイカイカリソウであるのかわからなくなってしまう」と頭を抱えられる著者の姿が浮かんできます。ちなみに現在ではこのオオバイカイカリソウはスズフレイカリソウともいわれ、バイカイカリソウとトキワイカリソウの交雑種群とされて、さまざまな中間形態のものも含まれると解説されています。昭和4年に出版の吉野善介の名著「備中植物誌」にはバイクワイカリとイカリサウだけでオオバイクワは名も出ないのは当然でオオバイクワが認識発表されたのは1932年(昭和7年)のことであった。ホソバナコバイモの記事に著者はこの初採集は阿哲郡草間村で赤木敏太郎氏が発見し、大正3年小泉源一博士が「新撰植物図編第二編第一集」に発表のものと解説されるので、前記備中植物誌にみると赤木氏は阿哲郡草間村姫原の人で郡内小学校教員であったことが判り、ほかにチョウジガマズミ、ヤマトレンギョウを発見しておられることが知られます。今珍稀危惧種とされるほどに減少したオグラセンノウも美しい写真で紹介され、岡山県では小坂弘氏が大正9年8月阿哲郡哲西町で採集されたものなどと、この種の発見史にも触れられ、さらに新見市の唐松小学校の記事はこの小坂氏の考案になるヒメコマツが図案化されたものと別頁に記されています。チョウジガマズミについて、村越氏は「集成新植物図鑑」のこの種についての記載が「大木にして云々。葉が対生する様殆ど丁字形をなせるの観あり故に本和名あり」とは全くの誤認であると広く万卷に当たられた姿勢を偲ぶことができます。

さらに昭和56年には岡山文庫100として「岡山の樹木」を著されています。今はひろく庭木に導入されて普及しているオオカナメモチが同県東部に大久保一氏によって発見されたことなども記され、17年前の「岡山の植物」に縁を得て多くの知己を得たことを喜ばれ、殊に岡山の植樹祭には天皇陛下の御散策の御相手を務めた光栄を生涯忘れることはできないと自序されています。

学者の論文は容易に民間同好素人の目には触れないことが多く無縁であることが多いが西原さんのような自ら素人をうたって、たのしく親しみやすい一般啓蒙書を残されたことは遠近にかかわらず著者の知の領布にあずかる学徳の余沢がいついまでも消えることがないことを痛感して、親しかった同好の友西原さんと今一度一献を傾けることのない人の世のさみしさを痛恨して岡山の人西原礼之助さんを偲びます。

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