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Studies on the Asian Eupatoria
II. Cytogeography of *Eupatorium chinense* subsp. *sachalinense* var. *oppositifolium*

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The examination of 1976 herbarium specimens of *Eupatorium chinense* subsp. *sachalinense* var. *oppositifolium* and 908 of var. *sachalinense* revealed their distinct geographical and ecologial distribution patterns. Var. *oppositifolium* includes two distinct groups: the diploid type and the polyploid one. The distribution of the diploid type is restricted to the "Sohayaki-Region", and its habitat appears to be restricted to fragile gravitational slopes and rocky areas which lack tall competitors. In contrast, the polyploid type is widely distributed throughout the Japan Archipelago. The polyploids grow successfully in recently cleared dry habitats and in repeatedly disturbed tall grass and forb communities. Climatic warming after the last-glaciation combined with explosive agricultural developments and the polyploids rapid and tall growth habits with agamospermous reproduction seem to have facilitated their northward migration and distributional expansion.

Karyotype analyses were made on 29 populations of var. *oppositifolium* which comprised eight cytotypes: 2x, 3x, 4x, 5x based on x=10, 3 chromosomally deficient polyploids and an aneuploid with 2n=39. Most populations exhibited various combinations of polyploid cytotypes. Different polyploid cytotypes show no apparent habitat preferences. None of the polyploid cytotypes appear to compete with each other in colonizing and exploiting newly disturbed habitats. This, together with their agamospermous propagation, rare sexuality and random association when colonizing, can result in an intricate mixture of various cytotypes within local populations.

Key words: Cytogeography — *Eupatorium* — Habitat preference — Polyploidy — Sohayaki-Region.

Accompanying the accumulation of phytogeographical data on the Japan Archipelago (e.g., Hara and Kanai, 1958, 1959; Horikawa, 1972, 1976), several floristic elements have been proposed from their distribution patterns and the origin of these patterns has been discussed (Koidzumi, 1931; Maekawa, 1949, 1957; Yamazaki, 1959; Fukuoka, 1965; Hotta, 1967, 1974; Koyama *et al.*, 1971; Murata and Koyama, 1976, 1980; Terao, 1979). Detailed studies on species with abundant variation and wide distributional range throughout the Japan Archipelago may contribute to understanding the origin and the direction of migration of these elements of the present Japanese flora. A cytogeographical approach can provide clues to certain important aspects of this problem when the ancestral type and its derivatives are well understood (Tateoka, 1974a, b). *Eupatorium chinense* subsp. *sachalinense* var. *oppositifolium* (this taxon was treated as *E. chinense* var. *simplicifolium* in the previous paper; see Murata and Koyama, 1982 on nomenclature) is widely and abundantly distributed throughout Japan and is known to have good chromosome markers (Watanabe *et al.*, 1982). Therefore, this taxon is considered a suitable subjects for a cytogeographical approach to the origin of floristic elements in Japan. Plants collected from the Rokko Mountains consist of seven cytotypes. These polymorphic karyotypes comprise a combination of 2x, 3x, 4x, 5x based on x=10 and partial chromosomal deficiency. The polyploid cytotypes have agamospermous reproduction. The diploid cytotype apparently occupies different habitats from the polyploids and is readily distinguishable from the latter in external morphology (Watanabe *et al.*, 1982). These differences make it possible to discriminate diploid from polyploid even in herbarium specimens. Accordingly, it is possible to examine the distributional differences between the diploid and polyploid cytotypes based on examination of a large number of herbarium specimens throughout Japan.

The purposes of this paper are 1) to construct distribution maps of diploid and polyploid cytotypes in Japan based on the herbarium specimens, 2) to elucidate the cytological structure of some local populations throughout the Japan Archipelago and 3) to discuss the development of the present distribution pattern of this variety.

Materials and Methods

Nomenclature of eupatoria in this paper follows Murata and Koyama (1982). The horizontal and vertical distribution maps of *E. chinenese* subsp. *sachalinense* and *E. chinense* subsp. *sachalinense* var. *oppositifolium* were published in 1972 by Horikawa (treated as *E. chinense* var. *sachalinense* and *E. chinense* var. *simplicifolium*, respectively). These maps, however, lack voucher specimens, hence his identifications can not be reexamined. On the other hand, most of the herbarium specimens examined lack altitudinal information. Consequently, the distribution maps in this paper were compiled by pooling the data on Horikawa's map (white circle) with those from herbarium specimens (black circle). The maps were constructed by Horikawa's method (1972); the horizontal distribution maps are divided into squares each of which corresponds to the area of a Govermental "topographic map" of 1/50000. This unit square covers an area 10 minutes in latitude by 15 minutes in longitude (about 18.5 km S-N × 22.82 km W-E in the square on lat. 35 N). A unit square of the vertical distribution maps covers 10 minutes in latitude and 100 m in altitude. Occurrence of a plant within a square is indicated by one circle irrespective of the number of known localities. A total of 1976 herbarium specimens of var. *oppositifolium* and 908 of var. *sachalinense* were examined. The specimens examined are preserved in the following herbaria; Botanical Gardens, University of Tokyo (TI), National Science Museum, Tokyo (TNS), Makino Herbarium, Tokyo Metropolitan University (MAK), Faculty of Science, Kanazawa University (KANA), Department of Botany, Kyoto University (KYO), Department of Biology, Osaka University (OU)*, Osaka Museum of Natural History (OSA), Department of Biology, Shoei Junior College (SHO)*, Biological Institute, Kobe University (KOB)* and Yamaguchi Prefectural Museum (YAM)*. Representative specimens cited have been listed in north-south order in the Appendix. In herbarium specimens, discrimination is possible between diploid and polyploids, but impossible between various levels of polyploidy. Consequently, the polyploids are treated collectively on the distribution maps. The collection sites for cytological examination are shown in Table 1 and Fig. 7. A total of 1024 individuals from 29 localities were examined. All of these individuals were typical var. *oppositifolium* with opposite, oblong-ovate and not dissected leaves, and any intermediate plants between this variety and other taxa were excluded from this study. The voucher specimens examined cytologically are housed in the herbarium of Kobe University. .The cytological techniques used were identical to those reported by Watanabe (1981).

Results and Discussion

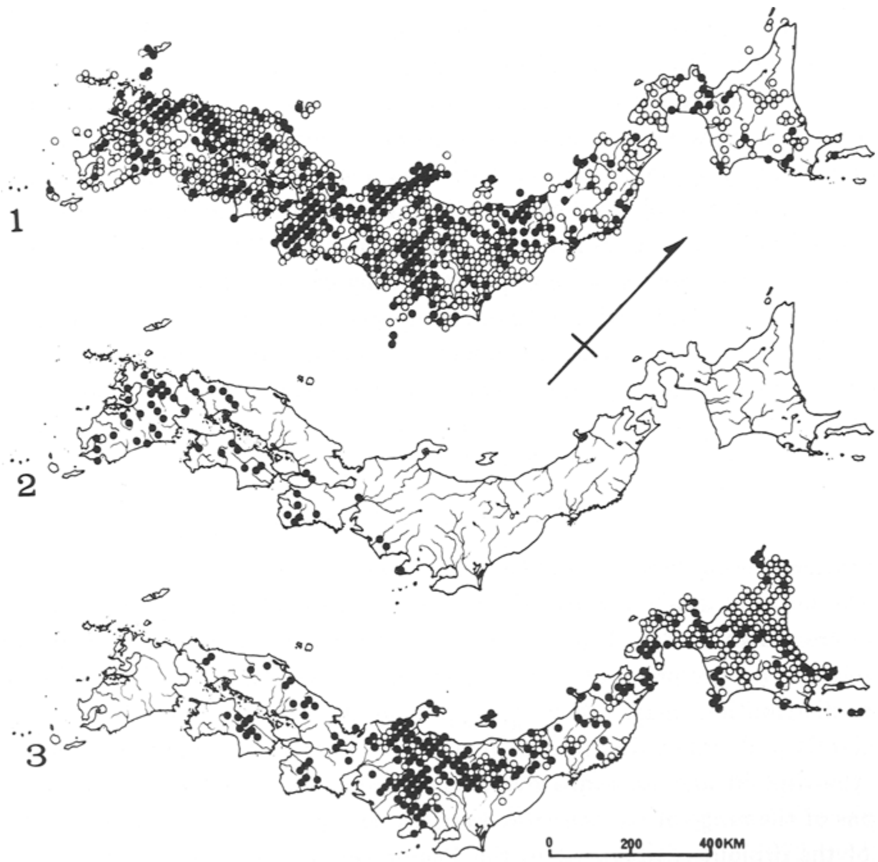
Distributional differences between the diploid and polyploid cytotypes

The horizontal and vertical distributions of diploid and polyploid var. *oppositifolium* are shown in Figs. 1, 2, 4, and 5. The horizontal and vertical distributions of var. *sachalinense* are presented for comparison with var. *oppositifolium* (Figs. 3 and 6). These distribution maps show that polyploid var. *oppositifolium* is much more abundantly and widely distributed than diploid ; the polyploid extends further north than the diploid and its range overlaps considerably with the southern and lower margins of the range of var. *sachalinense*. On the other hand, the horizontal distribution of the diploid is restricted to the Pacific side of southwestern Japan known as "Sohayaki-Region" of the floristic divisions of Japan (Koidzumi, 1931 ; Hotta 1974 ; Murata and Koyama, 1976 etc.) and overlaps with the range of var. *sachalinense* only in restricted areas of southwestern Japan. As for the vertical distribution in southwestern Japan, the polyploid extends from near sea level to about 2000 m alt., while the diploid is found only above 500 m alt. except in the Rokko Mountains (Watanabe *et al*., 1982) and in areas between the upper altitude warm-temperate zone and the lower altitude cool-temperate zone.

Difference in habitat preference

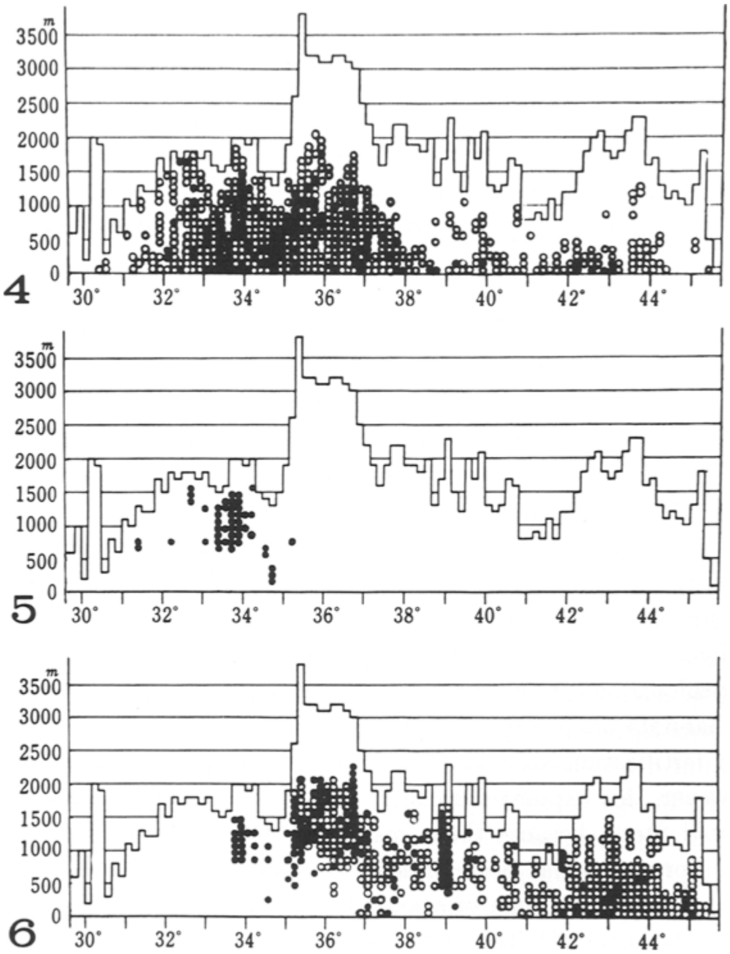
In the previous report (Watanabe *et al*., 1982), the difference in habitat preference between diploid and polyploid var. *oppositifolium* was confirmed in the populations of the Rokko Mountains : the diploid is restricted to fragile gravitational slopes and rocky areas which are poor in species and lack tall competitors while the polyploid occurs widely and is often associated with tall grasses and forbs such as *Miscanthus sinensis*. During the present study, such differences between the habitats of the diploid and the polyploid were more clearly confirmed in general.

* These acronyms are defined here. Others follow Index Herbariorum (ed. 7).



Figs. 1-3. The horizontal distribution of *E. chinense* subsp. *sachalinense* var. *oppositifolium* and var. *sachalinense*. 1 : polyploid-like var. *oppositifolium*. 2 : diploid-like var. *oppositifolium* ; note that its distribution is restricted to the southwestern parts of Japan. 3 : var. *sachalinense*. Open circles represent the data on Horikawa's map ; closed circles that from herbarium specimens.

Diploid var. *oppositifolium* usually grows on gravelly slopes or rocky areas with shallow soil depth. It is not considered to be a member of the understory herbs which are closely associated with forest vegetation and well-adapted to its closed environment. The habitat preferred by the diploid is on edges of or gaps in deciduous or mixed deciduous forests and it is in this sense that diploid var. *oppositifolium* is considered associated with forest vegetation. On the other hand, the polyploid var. *oppositifolium* is not associated with any characteristic forest vegetation but with the tall grass and forb community that develops in disturbed places such as roadsides or clearings, although it is found in the same climatic zone as warm-temperate evergreen and cool-temperate deciduous forests. It is considered less adapted to fragile gravelly slopes or rocky areas than the diploid, but is obviously superior in colonizing newly



Figs. 4–6. The vertical distribution of *E. chinense* subsp. *sachalinense* var. *oppositifolium* and var. *sachalinense*. 4 : polyploid-like var. *oppositifolium*. 5 : diploid-like var. *oppositifolium* ; note that its range is being encroached upon from both sides : from the upper and northern side by var. *sachalinense* and from the lower and southern side by polyploid-like var. *oppositifolium*. 6 : var. *sachalinense*.

cleared dry habitats.

At collection locality 22 (Mt. Ishizuchi), polyploid var. *oppositifolium* was observed to penetrate the area where diploids were found along the Ishizuchi-yama Highway. The construction of this highway (645–1493 m alt., total length 18.1 km) started in 1965 and finished in 1970. Accompanying this construction, natural forests composed of *Tsuga siedboldii*, *Abies firma*, *Fagus crenata*, *Abies homolepis*, etc. growing along the route of the highway were destroyed (Toyohara *et al.*, 1979). Since its construction, a number of ruderal and naturalized plants have penetrated these areas (Yamamoto, 1979). Polyploid var. *oppositifolium* was also found penetrating up to 900 m alt. in 1980. A considerable number of diploid seedlings, however, were still growing above 900 m alt. on areas surrounding the highway. In altitudes lower than 645 m, only polyploids were found and these occupied the habitats which were disturbed by man before the construction of the highway. Similar penetration of polyploids into the areas occupied by diploids or replacement of diploids by polyploids was observed at three additional localities where both the diploid and the polyploid were found (localities 14, 19, 26). In localities where the natural forest vegetation has not been disturbed by highway construction, only diploid var. *oppositifolium* was found (localities 13, 17, 23, 28).

Presumed distributional changes since the last glaciation

A widespread distribution of agamospermous polyploids compared with the restricted range of their diploid ancestor has been noted in various taxonomic groups (Babcock and Stebbins, 1938; Gustaffson, 1947; Stebbins, 1950, 1971; Grant, 1981) including eupatoria in southeastern United States (Sullivan, 1976). Recently, Bayer and Stebbins (1981, 1983) and also Wolf (1980) explained this distribution pattern, which was confirmed in *Antennaria* and *Arnica* growing in the areas severely affected by the successive advances and recessions of the Pleistocene ice sheets, in the following way. The ancestral diploid was probably restricted to a small area at the end of the last glaciation. Accompanying the glacial recession, a large number of open habitats, suitable for colonizing species, developed. The agamospermous polyploids colonized those open habitats successfully, whereas the sexual diploids were not good colonizers due to their fertilization loads and remained in their previously occupied, restricted areas. However, this explanation can not be applied to the eupatoria of the southeastern United States because there has never been glaciation there. A somewhat different interpretation has been presented by Sullivan (1976) for the widespread distribution of polyploid eupatoria and the restricted distribution of their diploid relatives in southeastern United States. According to her, newly exposed terraces of the Coastal Plain revealed by a falling sea level due to glaciation during the Pleistocene could have provided suitable habitats for the survival and spread of polyploid *Eupatorium* species at the expense of their diploid ancestors.

Since the Japan Archipelago was not covered by major ice sheets and only some high mountains in central Honshu and Hokkaido were icecapped during the last glacial period (Hashimoto and Minato, 1955; Kobayashi, 1958; Ono and Hirakawa, 1975), distributional changes of plants during the ice age in Japan, including the present diploid and polyploid assemblage of *Eupatorium*, were evidently different to a considerable extent from those in the severely glaciated areas. Likewise, Sullivan's explanation can be only partly applicable to the history of Japanese var. *oppositifolium* as it does not have a center of distribution in coastal regions as reported for North American eupatoria by Sullivan (1976).

The postglacial history of the vegetation of the Japan Archipelago is summarized as follows. After the last glacial period (maximum about 15000 yr. ago), the temperate deciduous forest began to migrate northward and to higher elevations from coastal refugia as a result of the climatic warming. By 7000–5000 yr. ago these forests had disappeared from the lowlands of southwestern Japan which had been invaded by warm-temperate evergreen forests (Tsukada, 1982a, b, c). Accompanying this migration, the overall distribution of eupatoria is assumed to have expanded northward and to higher elevation along with the distribution of many other temperate species. The present ranges of diploid var. *oppositifolium* and of var. *sachalinense* are assumed to have been established during this expansion era, because both are associated with naturally open or half-shaded communities on fragile gravitational slopes and rocky areas. On the other hand, it is not plausible that polyploid var. *oppositifolium* acquired abundant niches at this time because the Japan Archipelago is assumed to have been covered by closed forests throughout this era. As stated above, polyploid var. *oppositifolium* grows essentially in open or half-shaded places in disturbed habitats. Therefore, its distribution is considered to have been much restricted during the forest migration era. The expansion of the range of polyploid var. *oppositifolium* may be due to the expansion of disturbed areas due to growing human activities such as agricultural developments, public works, and so forth from the southward and coastal regions northward and to higher elevations. According to pollen analyses (Tsukada, 1963, 1982a), the beginning of pine pollen increase is about 2000 yr. ago in southwestern Japan, 1500 yr. ago in central Japan, and 800 yr. ago in northern Honshu. The pine pollen increase is a prominent stratigraphic marker and the delayed pine increase is certainly related to the expansion of intensified agricultural activities from the southwest to the northeast. Slash- and burn-agriculture had expanded throughout the Archipelago by 3000 yr. ago, and rice farming had already been initiated in the southwest by 2000 yr. ago, and in central Japan by 1500 yr. ago (Tsukada, 1981). Accompanying this intensified growth of human activity, the geographical distribution of polyploid var. *oppositifolium* is considered to have expanded quickly. The quick spread of polyploid var. *oppositifolium* into newly opened dry habitats may be primarily attributed to its formidable colonizing ability; resulting from its copious agamospermous reproduction and its ability to compete with tall grasses and forbs due to its rapid growth and tall stem.

In contrast, the favorite habitats of the diploids have been reduced by human activities. The diploid is not regarded as a good colonizer due to the low fecundity of its achenia, slow growth and shorter height. In newly opened habitats, it is easily outcompeted by taller rapidly growing competitors. The south slope of the Rokko Mountains rising precipitously from the Inland-Sea conserves the habitats of the diploid at an unusually low altitude.

Cytogeography of polyploid cytotypes

In a previous study, 13 var. *oppositifolium* populations in a small restricted area of the Rokko Mountains were examined and were found to consist of a total of six polyploid cytotypes and one diploid (Watanabe *et al.*, 1982). From this arise the questions whether this polyploid polymorphism is confined to this small area, or prevails over the whole distribution of this variety, and whether or not there are any particular occurrences of certain polyploid cytotypes in certain regions. To elucidate

Table 1. Frequencies of eight cytotypes of *E. chinense* subsp. *sachalinense*

Locality No.	Locality	Total No. Plants Examined	C_1 2n=20
1	Mt. Kunimiyama, Alt. 60-80 m, Memuro-cho, Kasai-gun, Hokkaido Pref.	25 (1.000)	—
2	3-go-nishi-5-sen, Alt. 60-80 m, Otofuke-cho, Kato-gun,Hokkaido Pref.	31 (1.000)	—
3	Mt. Moiwayama, Alt. 60-100 m, Moiwashita, Sapporo-City, Hokkaido Pref.	32 (1.000)	—
4	Poroto-Lake, Alt. 20 m, Shiraoi-cho, Shiraoi-gun,Hokkaido Pref.	28 (1.000)	—
5	Mt. Sokuryoyama, Alt. 80-150 m, Yamate-cho, Muroran-City, Hokkaido Pref.	44 (1.000)	—
6	Mt. Takakurayama, Alt. 50-80 m, Hanaizumi-cho, Nishiiwai-gun, Iwate Pref.	36 (1.000)	—
7	Onagawa, Alt. 20-50 m, Onagawa-cho, Oga-gun, Miyagi Pref.	7 (1.000)	—
8	Narita, Alt. 50 m, Ootarai-cho, Higashiibaragi-gun, Ibaragi Pref.	20 (1.000)	—
9	Mt. Kakutayama, Alt. 0-50 m, Maki-machi, Nishikanbara-gun, Niigata Pref.	33 (0.999)	—
10[1)]	Mts. Rokkosan, Alt. 40-560 m, Kobe-City, Kawanishi-City, Nishinomiya-City, Hyogo Pref.	265 (1.001)	41 (0.155)
11	Mt. Tonomine, Alt. 600-900 m, Oogochi-cho, Shiso-gun, Hyogo Pref.	8 (1.000)	—
12	Is. Nushima, Alt. 80-100 m, Nantan-cho, Mihara-gun, Hyogo Pref.	8 (1.000)	—
13	Mt. Oodaigahara, Alt. 1100-1500 m, Kawakami-mura, Yoshino-gun, Nara Pref.	17 (1.000)	17 (1.000)
14	Mt. Tamakiyama, Alt. 800-1050 m, Totsugawa-mura, Yoshino-gun, Nara Pref.	36 (1.001)	29 (0.806)
15	Sei-Hikogase Shurigawa, Alt. 50-600 m, Kanaya-cho, Arita-gun, Wakayama Pref.	40 (1.000)	—

var. *oppositifolium* from 29 localities throughout the Japan Archipelago

Cytotypes						
C_2 2n=30	C_3 2n=30	C_4 2n=40	C_5 2n=40	C_6 2n=50	C_7 2n=50	C_8 2n=39
1 (0.040)	—	24 (0.960)	—	—	—	—
—	—	30 (0.968)	—	—	—	1 (0.032)
4 (0.125)	—	11 (0.344)	—	17 (0.531)	—	—
—	—	28 (1.000)	—	—	—	—
17 (0.386)	—	23 (0.523)	—	4 (0.091)	—	—
—	3 (0.083)	31 (0.861)	2 (0.056)	—	—	—
—	—	7 (1.000)	—	—	—	—
—	—	20 (1.000)	—	—	—	—
4 (0.121)	1 (0.030)	27 (0.818)	—	1 (0.030)	—	—
69 (0.260)	2 (0.008)	102 (0.385)	26 (0.098)	10 (0.038)	15 (0.057)	—
3 (0.375)	5 (0.625)	—	—	—	—	—
6 (0.750)	—	2 (0.250)	—	—	—	—
—	—	—	—	—	—	—
1 (0.028)	—	4 (0.111)	2 (0.056)	—	—	—
9 (0.225)	—	7 (0.175)	24 (0.600)	—	—	—

Table 1.

Locality No.	Locality	Total No. Plants Examined	C_1 $2n=20$
16	Nakaban, Alt. 160 m, Hongu-cho, Higashimuro-gun, Wakayama Pref.	23 (1.000)	—
17	Nishinotani, Alt. 150-200 m, Kaita-cho, Aki-gun, Hiroshima Pref.	40 (1.000)	—
18	Sandankyo, Alt. 500-600 m, Togochi-cho, Yamagata-gun, Hiroshima Pref.	39 (1.000)	39 (1.000)
19	Nagoro-Mt. Tsurugisan, Alt. 900-1400 m, Iyayama-mura, Miyoshi-gun, Tokushima Pref.	56 (1.000)	53 (0.946)
20	Mt. Shiragayama, Alt. 500-1000 m, Motoyama-cho, Nagaoka-City, Kochi Pref.	25 (1.000)	—
21	Mt. Joyama, Alt. 60-90 m, Joyama-cho, Kochi-City, Kochi Pref.	18 (1.000)	—
22	Ishizuchi Highway, Alt. 500-1400 m, Omogo-mura, Kamiukena-gun, Ehime Pref.	34 (0.999)	24 (0.706)
23	Mt. Koshozan, Alt. 200-500 m, Amagi-City, Fukuoka Pref.	17 (1.000)	—
24	Mt. Homanzan, Alt. 700-860 m, Dazaifu-cho, Tsukushi-gun, Fukuoka Pref.	32 (1.000)	32 (1.000)
25	Shioji, Alt. 100-400 m, Dazaifu-cho, Tsukushi-gun, Fukuoka Pref.	34 (0.999)	—
26	Mt. Raizan, Alt. 700-900 m, Maebaru-cho, Itoshima-gun, Fukuoka Pref.	38 (1.000)	29 (0.763)
27	Shiroyama, Alt. 50 m, Katsumoto-cho, Iki-gun, Nagasaki Pref.	2 (1.000)	—
28	Mt. Ookueyama-Mtz Goyodake7 Alt. 1400-1500 m, Katagawa-cho, Higashiusuki-gun, Miyazaki Pref.	30 (1.000)	30 (1.000)
29	Maruo-Hayashida, Alt. 500-700 m, Makizono-cho, Aira-gun, Kagoshima Pref.	6 (0.999)	—
Total number of plant examined (Relative frequency)		1024 (1.000)	294 (0.287)

[1] Cited from Watanabe *et al.* (1982).
Numbers in brackets are relative frequencies

Continued

Cytotypes						
C_2 2n=30	C_3 2n=30	C_4 2n=40	C_5 2n=40	C_6 2n=50	C_7 2n=50	C_8 2n=39
10 (0.435)	—	9 (0.391)	4 (0.174)	—	—	—
1 (0.025)	—	39 (0.975)	—	—	—	—
—	—	—	—	—	—	—
—	—	3 (0.054)	—	—	—	—
1 (0.040)	1 (0.040)	15 (0.600)	8 (0.320)	—	—	—
7 (0.389)	—	11 (0.611)	—	—	—	—
1 (0.029)	—	8 (0.235)	1 (0.029)	—	—	—
4 (0.235)	—	13 (0.765)	—	—	—	—
—	—	—	—	—	—	—
6 (0.176)	—	24 (0.706)	—	3 (0.088)	1 (0.029)	—
2 (0.053)	—	7 (0.184)	—	—	—	—
2 (1.000)	—	—	—	—	—	—
—	—	—	—	—	—	—
2 (0.333)	—	2 (0.333)	2 (0.333)	—	—	—
150 (0.146)	12 (0.012)	447 (0.437)	69 (0.067)	35 (0.034)	16 (0.016)	1 (0.001)

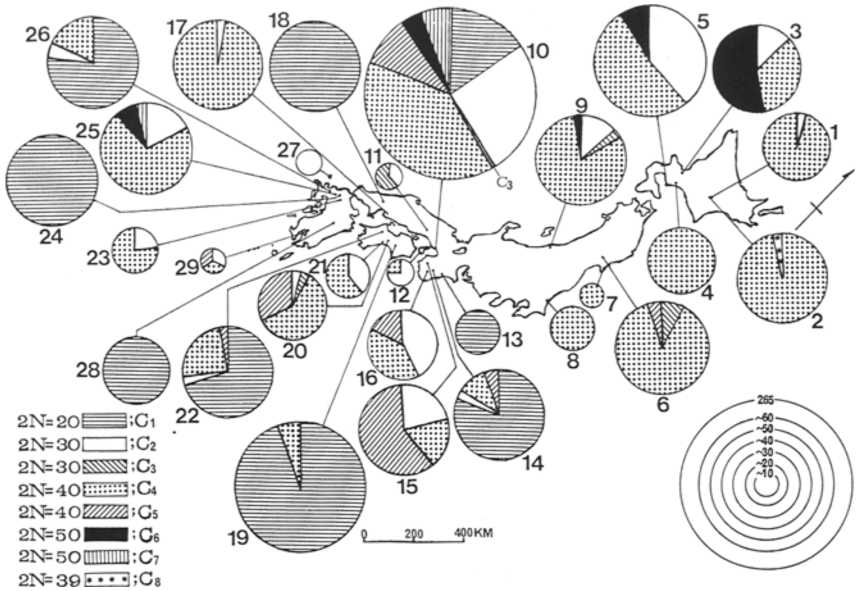
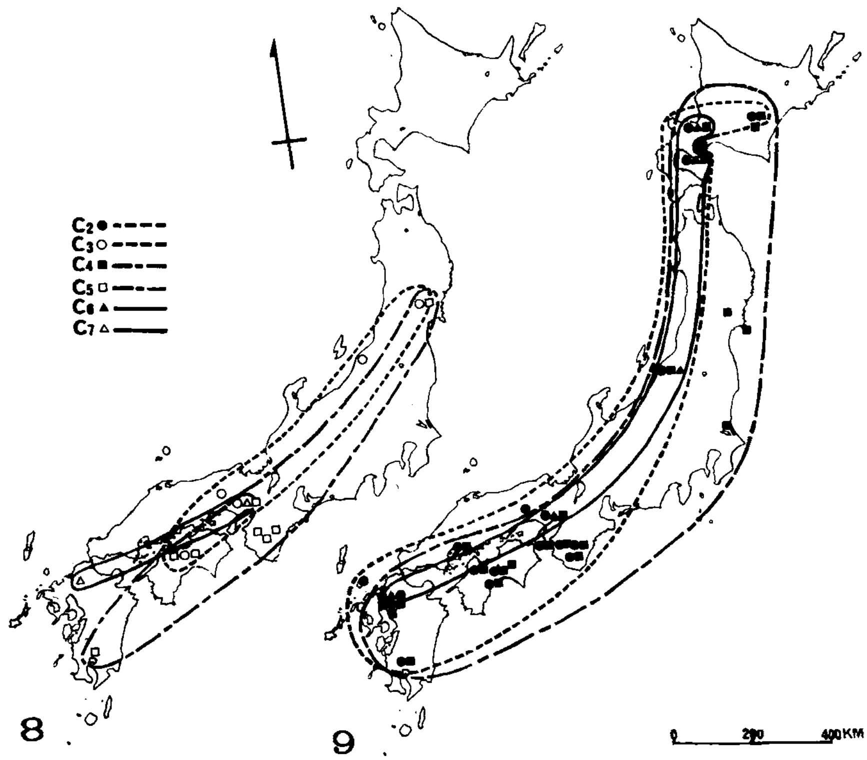


Fig. 7. Localities of the populations studied and fan diagrams of cytotype structure of each population of *E. chinense* subsp. *sachalinense* var. *oppositifolium*. The size of a circle corresponds to the number of plants observed in each locality. Locality numbers correspond to those appearing in Table 1.

these points and to confirm the diploid distribution pattern drawn from herbarium specimens, karyotype analyses were made for a total of 1024 individuals collected from 29 localities throughout the Japan Archipelago (Table 1). The karyological structure of the respective populations is represented by fan diagrams in Fig. 7. The collections were made more intensively in the warm-temperate to the cool-temperate zone of the "Sohayaki-Region" than in other areas to elucidate the frequency of diploid occurrences in this area. The present population census, including the previous report (Watanabe *et al.*, 1982), revealed 8 different cytotypes. The eighth cytotype, designated as C8, is an aneuploid with $2n=39$ from the locality 2. Minor karyotypic variations have been found at locality 5. One of the C4 plants had a slightly larger satellite than usual and one of C2 plants had three distinct satellite chromosomes. So far as examined, the plants assumed to be diploid from their growth habit and external morphology proved to be diploid cytologically and occurred from the upper altitude warm-temperate to the cool-temperate zone of the "Sohayaki-Region". Figs. 8 and 9 show the collection locations and a tentative outline of the distribution area of the various polyploid cytotypes. General distribution patterns can be read from these maps; however, the frequency of these cytotypes in each locality is very low except for C4 and C2, and further surveys in other areas are required. Among the six polyploid cytotypes, the tetraploid C4 was most frequent (61.2% of the polyploids) and widespread, followed by C2 (20.6%). The triploid C2 has been found throughout Japan except on the Pacific side of the Tohoku and Kanto districts. The pentaploid



Figs. 8 and 9. Outlines of the distribution areas of the various cytotypes of *E. chinense* subsp. *sachalinense* var. *oppositifolium*. 8: Cytotypes 3, 5 and 7 with a deficient marker chromosome. 9: Cytotypes 2, 4 and 6.

C6 was discovered in only 5 localities: Shioji and the mountains Moiwayama, Sokuryo-yama, Kakutayama and Rokkosan. The frequencies of chromosomally deficient cytotypes C3, C5 and C7 were relatively low but they show a wide range from Kyushu to the Tohoku district. They were not found at all among the 160 plants examined from Hokkaido. The distribution of a deficient marker chromosome in these cytotypes is considered as convincing evidence that agamospermatic dispersal and rare sexuality effectively produce widespread cytological polymorphism in this variety as it is highly improbable that such chromosomally deficient mutations could arise independently at many different localities and at several ploidy levels. The pentaploid C6 grows sympatrically with triploid C2 and tetraploid C4 throughout its range; the chromosomally deficient triploid C3 and/or pentaploid C7 with tetraploid C5 at localities 6, 10 and 20. It is suggested that they could arise independently at different localities by means of rare sexuality.

The populations at localities 4, 7, 8 and 27 are pure C2 or C4. The remaining polyploid populations exhibit various combinations of cytotypes irrespective of their population sizes. Different polyploid cytotypes show no different habitat preferences. The various polyploid cytotypes are assumed not to compete with each other in colonizing and exploiting newly disturbed habitats. This, together with their agamospermous propagation, rare sexuality and random association when clonizing can result in intricate mixtures of various cytotypes within local populations based on their particular histories in disturbed and temporary habitats.

The distributional patterns of various polyploid cytotypes are consistent with the above-mentioned hypothesis that the explosive geographical expansion of this variety into its present range began at south-western parts of Japan and proceeded to the northeast during a recent geological era characterized by growing human activities. Before this expansion era, polyploid cytotypes may have originated and survived in much more restricted habitats during glacial and postglacial periods.

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References

BABCOCK, E.B. AND G.L. STEBBINS. 1938. The American species of *Crepis*. Carnegie Inst. Washington Publ. **504**: 1-199.

BAYER, R.J. AND G.L. STEBBINS. 1981. Chronosome numbers of North American species of *Antennaria* GAERTNER (Asteraceae: Inuleae). Amer. J. Bot. **68**: 1342-1349.

——— AND ———. 1983. Distribution of sexual and apomictic populations of *Antennaria parlinii*. Evolution **37**: 555-561.

FUKUOKA, N. 1966. On the distribution patterns of the so-called Japan Sea elements confined to the Japan Sea Region. J. Geobot. **15**: 63-80 (in Japanese).

GRANT, V. 1981. Plant Speciation (2nd ed.). Columbia Univ. Press, New York.

GUSTAFFSON, A. 1947. Apomixis in higher plants. III. Biotype and species formation. Lunds Univ. Arsskr. N.F. Avd. 2. **43**: 183-370.

HARA, H. AND H. KANAI. 1958. Distribution Maps of Flowering Plants in Japan 1. Inoue Book Co., Tokyo.

——— AND ———. 1959. Distribution Maps of Flowering Plants in Japan 2. Inoue Book Co., Tokyo.

HASHIMOTO, S. AND M. MINATO. 1955. Quaternary geology of Hokkaido I. On the ice ages and postglacial age of the Hidaka Mountain Range. J. Fac. Sci. Hokkaido Univ., Ser. IV (Geology) **9**: 7-20.

HORIKAWA, Y. 1972. Atlas of the Japanese Flora I. Gakken, Tokyo.

———. 1976. Atlas of the Japanese Flora II. Gakken, Tokyo.

HOTTA, M. 1967. Some phytogeographical problems of Japanese Islands. Michurin Biology **3**: 122-135 (in Japanese).

———. 1974. History and Geography of Plants (Evolutionary Biology in Plants III) p. 1-400. Sanseido Co., Ltd., Tokyo (in Japanese).

KOBAYASHI, K. 1958. Quaternary glaciation of the Japan Alps. J. Fac. Lib. Art. Sci. Shinshu Univ. **8**: 13-67.

KOIDZUMI, G. 1931. Zengen (Preface). *In* : Mayebara, Florula Austro-Higoensis (Private publication, in Japanese).

KOYAMA, H., N. FUKUOKA AND N. KUROSAKI. 1971. Taxonomic and geographic studies on the Japan-Sea elements. I. On the northern species (Sympetalae). Mem. Natn. Sci. Mus. Tokyo **4** : 87-94 (in Japanese).

MAEKAWA, F. 1949. Makinoesia and its bearing to Oriental Asiatic flora. J. Jap. Bot. **24** : 91-96 (in Japanese).

————. 1957. Curious distribution of *Sciadopitys* and its suggestive meaning. J. Jap. Bot. **32** : 65-68 (in Japanese).

MURATA, G. AND H. KOYAMA. 1976. On the "Sohayaki element" defined by Dr. G. Koidzumi. Mem. Natn. Sci. Mus. Tokyo **9** : 111-120 (in Japanese).

———— AND ————. 1980. Characteristic in the flora of the Pacific side of Japan. Mem. Natn. Sci. Mus. Tokyo **13** : 155-168 (in Japanese).

———— AND ————. 1982. On *Eupatorium* of Japan. Acta Phytotax. Geobot. **33** : 282-301 (in Japanese).

ONO, Y. AND K. HIRAKAWA. 1975. Environments forming topography in the vicinity of the Hidaka Mountains during the Wurm glacial period. The Geograph. Rev. Japan **48** : 1-26 (in Japanese).

STEBBINS, G.L. 1950. Variation and Evolution in Plants. Columbia Univ. Press, New York.

————. 1971. Chromosomal Evolution in Higher Plants. Edward Arnold Ltd., London.

SULLIVAN, V.I. 1976. Diploidy, polyploidy, agamospermy among species of *Eupatorium* (Compositae). Can. J. Bot. **54** : 2907-2917.

TATEOKA, T. 1974a. Phytogeographical studies of *Calamagrostis sachalinensis* (Gramineae) I. Attributes of infraspecific races. Bot. Mag. Tokyo **87** : 138-147.

————. 1974b. Phytogeographical studies of *Calamagrostis sachalinensis* (Gramineae) II. Origin and dispersal. Bot. Mag. Tokyo **87** : 149-164.

TERAO, H. 1979. Phytogeographical and taxonomical studies on Japanese *Oxalis acetosella* s.l. Acta Phytotax. Geobot. **30** : 45-64.

TOYOHARA, G., H. ANDO AND H. SUZUKI. 1979. Change of the vegetation on Mt. Ishizuchi after the construction of a highway, "Ishizuchi Sky-line". Rep. Nature Conservation Soc. Japan **58** : 53-64 (in Japanese).

TSUKADA, M. 1963. Umbrella pine, *Sciadopitys verticillata* : Past and present distribution in Japan. Science **142** : 1680-1681.

————. 1981. The last 12000 years-vegetation history of Japan II. New pollen zones. Jap. J. Ecol. **31** : 201-215 (in Japanese).

————. 1982a. *Cryptomeria japonica* : Glacial refugia and last-glacial and postglacial migration. Ecology **63** : 1091-1105.

————. 1982b. Late-Quaternary shift of *Fagus* distribution. Bot. Mag. Tokyo **95** : 203-217.

————. 1982c. Late-Quaternary development of the *Fagus* forest in the Japanese Archipelago. Jap. J. Ecol. **32** : 113-118.

WATANABE, K. 1981. Studies on the control of diploid-like meiosis in polyploid taxa of *Chrysanthemum* I. Hexaploid *Ch. japonense* Nakai. Cytologia **46** : 459-498.

————, T. FUKUHARA AND Y. HUZIWARA. 1982. Studies on the Asian eupatorias I. *Eupatorium chinense* var. *simplicifolium* from the Rokko Mountains. Bot. Mag. Tokyo **95** : 261-280.

WOLF, S.J. 1980. Cytogeographical studies in the genus *Arnica* (Compositae : Senecioneae) I. Amer. J. Bot. **67** : 300-308.

YAMAMOTO, S. 1979. On the plants of Mt. Ishizuchi and its neighbours. Rep. Nature Conservation Soc. Japan **58** : 75-86 (in Japanese).

YAMAZAKI, T. 1959. Floristic distribution in the Japanese Islands. Nat. Sci. & Mus. **26** : 1-19 (in Japanese).

Appendix 1. Enumeration of voucher specimens for distribution maps

Eupatorium chinense subsp. *sachalinense* var. *oppositifolium.*

Diploid Type: *Shizuoka Pref.* Yamazaki 286; Shimizu July 31, 1929 & July 28, 1930; Oomura 120; Kimura Nov. 27, 1944(TI): TNS 43832(TNS): MAK 182145, 182160(MAK). *Gifu Pref.* Kanai Oct. 1, 1957(TI). *Hyogo Pref.* TNS 386055(TNS): Watanabe 614, 615, 617-622(KOB). *Nara Pref.* Tamura 9489, 9492(OU): Kodama 6863(OSA): Watanabe 723-744, 747-771, 774-781, 783, 790-792, 795, 801-829(KOB). *Wakayama Pref.* Koyama 909; TNS 38685, 108537 (TNS): Seto 6189(OSA). *Hiroshima Pref.* KANA 24784(KANA): Sato 8801(KYO): Watanabe 496-573(KOB). *Yamaguchi Pref.*: TNS 82937, 82938(TNS): Masaki 20154(KYO): Masaki 20153; Oka 32407; Nikai 12783(YAM). *Tokushima Pref.* Koidzumi 99591(TNS): Takafuji 744(KYO): Watanabe 358-478, 485, 487-495(KOB). *Ehime Pref.* Shibuya Aug. 5, 1958(TI): Murata 9308(KYO): Watanabe 281-324, 326-332, 335-343, 352(KOB): Takazu 24104(YAM). *Kochi Pref.* TI 1317281(TI): MAK 182163(MAK): Tagawa 2877(KYO): Hori 204(OSA). *Fukuoka Pref.* Hashimoto Aug. 25-26, 1952(TI): MAK 24351(MAK): Hotta 6132(KYO): Kurosaki 8592(KYO, SHO): Tsutsui 13047, 15626, 15884, 18253, 18568, 18583, 18593, 18628, 18656, 18659, 18837, 18873, 19093, 19099; Inoue 2313, 3558, 3634, 3716, 3728, 4096, 4099, 4109, 5063; Watanabe 30-148(KOB). *Saga Pref.* Tsutsui 21582, 21585(KOB). *Nagasaki Pref.* Midorikawa Oct. 7, 1976(TI): TNS 137857, 273499(TNS): Greatrex 193/38(KYO). *Kumamoto Pref.* Imae & Murakami 12599(KANA): Shimada 10825(KYO): Shimizu 4935(OSA). *Ooita Pref.* Kanai Oct. 31, 1958(TI): Yamamoto 4196: TNS 102147(TNS): Nakashima 101(KYO). *Miyazaki Pref.* TNS 105127(TNS): Takahashi 1047(KANA): Watanabe 1-29(KOB). *Kagoshima Pref.* Momiyama Oct. 4, 1958: Hashimoto Aug. 30, 1950(TI): KANA 19363(KANA): Sato 4269(KYO): Kodama 7340 (OSA).

Polyploid type: *Hokkaido.* Mizushima Sept. 25, 1943 & July 26, 1945; Matsumura July 31, 1899; Nakai Aug. 1928; TI 1321501, 1321502(TI): Goda 126; TNS 268589, 373798(TNS): MAK 135683, 24342(MAK): KANA 69669(KANA): Okamoto 553; Horikawa 490; Koyama 5628 (KYO): Sonobe 1236(OSA): Murata 2076(SHO): Watanabe 1052-1375(KOB). *Aomori Pref.* Kanai July 9. 1981(TI). *Iwate Pref.* Kanai Aug. 31, 1959 & Sept, 2, 1959(TI): TNS 176121(TNS): KANA 16654(KANA): Koyama 2485; Murata & Tabata 34; Iwatsuki 6151(KYO); Watanabe 968-1051(KOB). *Miyagi Pref.* Ogura July 30, 1914(TI); Ueno 23570(TNS); Watanabe 961-967(KOB). *Akita Pref.* Yatabe Aug. 1, 1887; Muramatsu Aug. 16, 1931(TI): TNS 213526, 213527(TNS): Mochizuki 844(KANA): Muramatsu 6(KYO). *Yamagata Pref.* Suzuki Aug. 7, 1937; Kanai Sept. 8, 1959(TI): Okuyama 7037; TNS 42805(TNS): MAK 54192, 107998, 153387-153389, 182138(MAK): KANA 740(KANA): Ogura 2494(SHO). *Fukushima Pref.* Hattori July 30, 1925(TI): MAK 107450, 182139, 182140; Shimizu 293(MAK): KANA 34342, 21519(KANA). *Ibaragi Pref.* MAK 107451, 182141, 182142(MAK): Sato 9047(KYO): Watanabe 943-960(KOB). *Tochigi Pref.* KANA 16345(KANA). *Gumma Pref.* Yahagi Aug. 6, 1968(TI): MAK 182143 (MAK): Murata 27425(KYO). *Saitama Pref.* Ohba 528(TI). *Chiba Pref.* Tamura Aug. 23, 1938(TI): MAK 8786, 183218(MAK): Wakana 10872(KANA). *Tokyo Met.* Ando 4172; Furusawa Oct. 1938; Mizushima July 7, 1946 & Sept. 15, 1946; TI 1320821(TI): Y. Jotani 286, 10757(TNS). *Kanagawa Pref.* Momiyama Oct. 1931 & Oct. 13, 1932; Furusawa Sept. 1937; Hisauchi 2249; Togashi Oct. 3, 1937(TI): TNS 250912(TNS). *Niigata Pref.* Yamazaki Aug. 25, 1946; Ohba & Akiyama 1627; Shimizu 18; Eguchi July 28, 1951 & Sept. 1, 1951; Yatabe July 29, 1886; TI 6566(TI): Kanai 731250; TNS 121932, 267319, 302553(TNS): Ajima 4455; KANA 19632, 52317, 52788, 53080(KANA): Hiroe 14293; Nitta 11578; Koyama 534(KYO): Watanabe 893-942(KOB): Ikegami 95378(YAM). *Toyama Pref.* Kurosaki 2646(TNS, KANA), 3982, 5082(KANA), 2587(KYO), 2082, 5073(SHO). *Ishikawa Pref.* Yamaoka Sept. 1948; Fukuda Oct. 11, 1976(TI): MAK 146583(MAK): Yamamori 401, 3461; Oura 1238, 1726; Nakagawa 640; Kikuchi 1028; Furuike 5995, 9046, 9054; Hashimoto 4276; Matsuda 575; KANA 2724, 13192, 16486, 24212, 28130, 34146, 37761, 37963, 38383, 40405, 52612, 52862, 56850, 57755, 57781, 57782, 60086, 61687, 61688, 63138, 65255, 67092, 71651, 73061, 73382, 85805, 94181, 94421, 94451(KANA): Kurosaki 3229, 3702(SHO): YAM 28008(YAM). *Fukui Pref.* KANA 28091, 28120, 28121, 37795, 52517, 58754, 72627, 73284, 73296(KANA): Murata 27387(KYO). *Yamanashi Pref.* Matsuda Sept. 24, 1955; Yamazaki Sept. 7, 1954; Yamazaki & Matsuda Oct. 10, 1954; Kanai Nov. 3, 1956(TI): MAK 107449, 182144(MAK). *Nagano Pref.* Hasegawa Sept. 16, 1967; Momose July 25, 1935, Aug. 8, 1931, Aug. 3, 1933, Aug. 23, 1933, Aug. 20, 1936; Yamazaki Sept. 30, 1944, July 31, 1954; Kanai 425; Asano 13095; TI 1323893, 1323895(TI): TNS 114887, 12266(TNS): MAK 5138, 8475(MAK): KANA 52287(KANA): Shimrzu 5703; Murata & Shimizu 1454(KYO): Fukuoka & Kurosaki 1775(KYO, SHO): Kadono 1054, 1061, 1070, 1121(KOB). *Gifu Pref.* Murata 14384, 14419; Hotta & Inamasu 48(KYO). *Shizuoka Pref.* Shimizu Aug. 30, 1929, Sept. 23, 1929, July 28, 1930, Aug. 8, 1930; Nakai Oct. 1935; Kanai 7489, Aug. 11, 1954, Sept. 17, 1954, Sept. 23, 1957(TI): TNS 43833(TNS): MAK 155141(MAK): KANA 58968(KANA). *Aichi Pref.* Asano 13056; Enomoto July 24, 1968(TI): Mimoro *et al.* 2083(TNS): Murata 7436, 13255; Ueda & Ito 87(KYO). *Mie Pref.* MAK 182146-182148(MAK). *Shiga Pref.* Ohba & Akiyama 1993; Hasegawa June 30 1968(TI): Soneda 38(TNS): KANA 58921(KANA). *Kyoto Pref.* Murata 19178(TI, TNS, MAK): Yamamoto(TI, TNS): KANA 6484(KANA): Kuwashima 18826, 26426; Nakai 3813; Nagai 20390; Hori 1087(OSA): Watanabe 889-892(KOB). *Osaka Pref.* Togashi 7908(TI): Inamasu 132(TNS, MAK): Tamura, Kimura & Kosuge 25149(OU): Okamoto 1446; Seto 3214, 6983, 6998; Kodama 5572, 8432; Nakajima 248(OSA). *Hyogo Pref.* Togashi Sept. 12, 1949, Sept. 9, 1956; Hirano Oct. 26, 1907, Sept. 3, 1910; Yoshio Sept. 24, 1933; Okamoto 19661(TI): MAK 182151-182153(MAK): KANA 69123(KANA): Kuwashima 21365; Kurosaki 5861(OSA): Seto 19769(KANA, OSA): Kurosaki 5360, 5423, 5861, 8035, 8420; Fukuoka & Kurosaki 1066, 1190, 1294, 2127, 2130(SHO): Watanabe 616, 623-718(KOB). *Nara Pref.* Ohashi *et al.* 594(TI): Fukuoka & Hotta 12(TNS): Kodama 6410, 6934; Seto 21972(OSA): Watanabe 719-722, 745, 746, 772, 773, 782, 784-789, 793, 794, 796-800(KOB). *Wakayama Pref.* Nakashima Sept. 1924; Okamoto 7708; Hiroe 14890(TI): Mitsuhashi 120(TNS): Satomi 13143; MAK 11797, 182150 (MAK): Mimoro, Tsugaru & Fujimoto 14844(KYO): Seto 6748; Mihashi 191(OSA): Watanabe 830-888(KOB). *Tottori Pref.* Ohba & Akiyama 2186(TI): Tanaka 20541(KYO). *Shimane Pref.* Honda Aug. 17, 1947(TI): Takagi 56410; TNS 338434(TNS): Nagai 11349; Hayashi 1817(KYO). *Okayama Pref.* MAK 182154, 182186 (MAK). *Hiroshima Pref.* Maekawa 57, 13870 (TI): Matsumoto 1047; Fujita 189(KYO): Okada 468(OU): Fukuoka 2900(SHO): Watanabe 594-613 (KOB). *Yamaguchi Pref.* Nikai 2874(TI): Oka 1817, 27101; TNS 45967, 45972, 45978, 82900, 260077, 260078, 323696(TNS): KANA 19632, 42710(KANA): Miake 8711, 9588; Oka 1816, 3524, 8113, 8837, 27102, 40157, 43907; Oda 2006; Wada 2006, 2010, 5357; Nikai 12783; YAM 50, 2461, 27582, 27926, 28008, 45494, 45625(YAM). *Tokushima Pref.* Koyama 1137(TNS): Murata 7655(KYO): Watanabe 479-484, 486(KOB). *Kagawa Pref.* Yamazaki Oct. 15, 1963; Kawasaki Aug. 5, 1957(TI): Oka 40157(YAM). *Ehime Pref.* Shibuya July 30, 1958(TI): MAK 24341(MAK): Murata 15032; Yamanaka 56448; Takahashi & Fujita 252(KYO): Watanabe 325, 333, 334, 345-351, 353-357(KOB). *Kochi Pref.* Yamaki 97482(TNS): MAK 153390, 179677, 183221(MAK): KANA 20285(KANA): Yamanaka 51075, 51564; Tagawa & Iwatsuki 2065(KYO): Watanabe 210-280(KOB). *Fukuoka Pref.* Fujimoto Aug. 23, 1952; Hashimoto Oct. 1952(TI): TNS 58040 (TNS): Tsutsui 15968, 15979, 16016, 17676, 17717, 17882, 18369, 18436, 18563, 18674, 18758, 18918, 19053, 19082, 19162, 19270, 21957, 21977; Inoue 2341, 3803, 3806, 3807, 3902, 3923, 3987; Watanabe 149-209(KOB). *Saga Pref.* Baba 23(KYO): Tsutsui 21580-21582, 21584, 21586, 21587, 21612, 21622(KOB). *Nagasaki Pref.* Hara & Kurosawa Oct. 9, 1977; Toyama Oct. 9, 1952; Hirata 443(TI): Koyama 2631; TNS 36400, 56409, 118119(TNS): MAK 24339(MAK): Shinagawa, 7, 19(KYO): Tsutsui 21629(KOB). *Kumamoto Pref.* Hatsushima & Sako 27079(MAK, KANA): Shimada 7483(KANA): Shimada 7393, 7482(KYO). *Miyazaki Pref.* Momiyama Oct. 10, 1958; Kanai Oct. 18, 1958 & Oct. 21, 1958(TI): TNS 24956(TNS): Hatsushima & Sako 26346 (MAK): Hatsushima, Sako & Kawanabe 22349; KANA 27064(KANA): Hotta 6560; Takahashi 1047; Fujita 159(KYO): Tsutsui 21498, 21542, 21545(KOB). *Kagoshima Pref.* TNS 40842(TNS): Hatsushima 21029; MAK 153391(MAK): Iwatsuki 3236(KYO): Tsutsui 21304, 21305, 21337, 21361(KOB): YAM 45494(YAM).

Eupatorium chinense subsp. *sachalinense*.

Hokkaido. Hiroe 7538; Takahashi 445; Mizushima Sept. 18, 1943, Oct. 8, 1943, July 26, 1945; Kanai July 18, 1956 & July 22, 1956; Takeda July 21, 1977; Hasegawa June 1962; Nakai Aug. 25, 1920 & Aug. 27, 1920; Koidzumi Aug. 1911, Aug. 1916; Yamada Aug. 11, 1909(TI): Koizumi 22114, 73715, 83932; Hemmi 1510; TNS 29688, 45572, 68869, 81391, 175319, 248440, 308016, 308078, 309287, 338920, 339435(TNS): Soma & Takahashi 526; MAK 99134, 99135, 128329, 182164(MAK): KANA 22028, 32386, 62702(KANA): Koyama 1681; Yamada 100; Takahashi 445; Yamamoto 173; Hiroe 7538; Ohwi 1123; Okamoto 68, 1329,; Naruhashi 2577; Shimizu 908; Momotani 508; Murata 9000, 9183, 37297; Wakabayashi, Kaku & Takahashi 179; Koyama & Fukuoka 3134; Fujita & Konno 210; Murata & Momotani 479(KYO): Kuwashima 16460(OSA): Watanabe 1500-1789(KOB). *Aomori Pref*. Ohashi 4708; Murata & Ohba 5501; Okamoto Oct. 1, 1953; Yamada & Sawada Aug. 17, 1905; TI 1312727(TI): TNS 105295(TNS): MAK 10707, 22902, 23123(MAK): KANA 14435(KANA): Okamoto 774; Koyama 779; Murata & Tabata 108(KYO). *Iwate Pref*. Yamada Aug. 15, 1907(TI): Okuyama 12759, 12760; Koyama 2485; TNS 12290(TNS): MAK 24338, 107455(MAK): Iwatsuki & Tamura 6397; Kitamura & Murata 412(KYO): Okada 787, 788(OU): Fukuoka 2842(SHO): Watanabe 1790-1864(KOB). *Miyagi Pref*. Ohashi July 24-26, 1963(TI): Okuyama 9288, TNS 375020(TNS): Ogura 2274(SHO). *Akita Pref*. Muramatsu July 22, 1931 & Aug. 21, 1933(TI): Henmi 6804, 6805; TNS 162892(TNS): Mochizuki 2140(KANA). *Yamagata Pref*. Ohashi 8698; Iwatsuki , Koyama & Inamasu 657(TI): Koidzumi 33357; Okuyama 2789, 7401(TNS): MAK 107457, 107458(MAK): KANA 27125, 30023(KANA): Koyama(KYO). *Fukushima Pref*. Nakahara July 25, 1904 & Aug. 26, 1904; Koizumi Aug. 1911; Tsuyama Sept. 29, 1968(TI): Koidzumi 82288, 100769(TNS): MAK 19906, 107456(MAK): KANA 23384(KANA): Ohwi & Tagawa 540(KYO). *Tochigi Pref*. Muramatsu 652; Mizushima Aug. 6, 1949; Ito July 3, 1933(TI): TNS 12289, 41603, 302560(TNS): MAK 8790, 8791, 104655, 127221, 183216(MAK): Makino 8791; KANA 2721, 2723, 2725, 2726(KANA): Hiroe 1204; Tagawa & Iwatsuki 1863(KYO): Tamura 3895(OU). *Gumma Pref*. Nishida July 14, 1950; Mizushima July 4, 1950; Ono July 3, 1948; Ono & Kobayashi 133001; TI 9830(TI): Yamamoto 4242; Okuyama 2058, 10135, 13665; Koidzumi 92161; TNS 133501, 162741(TNS): MAK 5137, 133001, 182929(MAK): KANA 86644(KANA): Ono & Kobayashi 133001; Ohwi & Tagawa 130, 133(KYO). *Saitama Pref*. TNS 40843(TNS). *Tokyo Metrop*. Yamazaki July 7, 1946 & July, 1, 1948; Mizushima July 7, 1946(TI): MAK 183223(MAK). *Kanagawa Pref*. Nakai Nov. 1926; Sawada 2248; Yamazaki Sept. 24, 1946(TI): MAK 8792(MAK). *Niigata Pref*. Yatabe Aug. 13, 1879, July 19, 1886, July 29, 1886, Aug. 1, 1886, Aug. 2, 1886(TI): Okuyama 10723, 23907, 52870; TNS 56408, 182038, 267318, 271125(TNS): MAK 8788(MAK): Ajima 3059, 4435; KANA 8835(KANA): Murata 6362, 6796; Shimizu 115; Nitta 11603; Ueda 150; Kitamura & Murata 2814(KYO): Kuwashima 16013(OSA): Ajima 3049 (SHO): Watanabe 1865-1927(KOB): Ikegami 88493, 94184(YAM). *Toyama Pref*. Nagai 59; Kanai Aug. 4, 1958(TI): MAK 57037, 107452, 182166(MAK): Ishioka 184; Kurosaki 2002, 5080; Sato 1948; Nagai & Takasu 32(KANA): Kurosaki 2081(KYO): Murata 3962(OSA). *Ishikawa Pref*. Nikai 2055(YI): MAK 12361(MAK): Oura 1093; Matsuda 783, 1984; Fujita 140, 224, 273, 374, 586; Masamune 8988, 11633, 16504; Nakagawa 394; Furuike 9053; Yamamori 3449; Hashimoto 5905; KANA 2722, 5106, 13708, 15027, 23480, 23741, 57756, 71649, 95572(KANA): Kurosaki 2893; Matsmura 2150(SHO). *Fukui Pref*. KANA 28112(KANA): Murata 294; Fukuoka 4844(KYO). *Yamanashi Pref*. Tateishi 2215; Iwatsuki 5186; Ohba 69829; Uematsu Aug. 1, 1949, Aug. 2, 1949, Aug. 3, 1949; Yamazaki Sept. 6, 1956; Matsuda Sept. 6, 1954(TI): Okuyama 14430, 102499(TNS): MAK 182165(MAK): Murata 12113(KYO): Tamura 8751(OU): Kodama 5256(OSA). *Nagano Pref*. Asano 2138, 2307, 3535, 10460, 11054, 13902; Mizushima July 22, 1947; Momose 566, 813, July 29, 1931, Aug. 3, 1933, July 27, 1934, July 23, 1935, July 30, 1935, Aug. 20, 1936; Kanai July 28, 1957, July 31, 1957, Sept. 19, 1959; Yamazaki & Asano 7543; TI 1323894, 1323896; Teramoto Aug. 27, 1947, Aug. 28, 1947,; Tateishi 331; Yamazaki & Ono Aug. 13, 1948; Katsumata Sept. 14, 1931; Furuya Aug. 13, 1950; Hasegawa July 24, 1964(TI): Mimoro & Tsugaru 934; Yamamoto 745; Koidzumi 8716, 12481, 48731; Okuyama 22047, 24339; Koidzumi 65339; TNS 12279, 43831, 55028, 64752, 106424, 114784, 238304, 260076, 309791, 322778(TNS): Minemura 1463; MAK 5134, 8476, 11794, 52383, 107459, 126946, 135331, 153386, 179675, 183212, 183213(MAK): Iwatsuki, Fukuoka & Naruhashi 31, KANA 33522, 33694, 33729(KANA); Fujita & Kato 2; Murata & Koyama 92; Ohwi 8282; Tateishi 331;

Murata 11867, 27572 ; Wakabayashi, Takahashi & Naito 36(KYO) : Seto 21636(OSA) : Matsumura 5708(SHO) : Kadono 1053(KOB) : YAM 41734(YMA). *Gifu Pref*. Kanai June 20, 1956 ; Koizumi Aug. 1910(TI) : TNS 270178, 313479, 331974(TNS) : Mitsumura 427, 666 ; Yonezawa 210(KANA) : Fukuoka & Yamashita 86(KYO) : Seto 10918(OSA). *Shizuoka Pref*. Kanai 7490, July 18, 1954 ; Tateishi 2256 ; Nakai July 24, 1924 ; Yamazaki June 13, 1954 ; Hisauchi Aug. 22, 1934 ; Shimizu 9 ; Hayata Aug. 8-9, 1924, July 26, 1924, July 27, 1924, Aug. 29, 1924 ; Tsuyama July 14, 1934(TI) : Yamamoto 2453 ; Koyama *et al*. 49, 62 ; TNS 265987(TNS) : Konta & Matsumoto 111 ; MAK 153385(MAK) : Hutoh 24964 ; Saito, Yuasa & Konta 1981(KYO). *Aichi Pref*. TNS 133887, 138365, 305114(TNS) : KANA 68972(KANA). *Mie Pref*. KANA 52820(KANA). *Shiga Pref*. Hashimoto 5313 ; Kitamura & Murata 3350(TNS) : MAK 104098(MAK) : Watanabe 1928-1972 (KOB). *Kyoto Pref*. Nakai July 15, 1940 ; Yoshino Sept. 13, 1941(TI) : Tagawa 2287 ; Okuyama 13094 ; TNS 241049, 241519(TNS) : MAK 183215(MAK) : Nagai 20820(OSA). *Hyogo Pref*. Hiroe 7427 ; Kurosaki 7854(TI) : TNS 37978(TNS) : Kitamura & Murata 629(KYO) : Seto 12671, 15243, 17548(OSA) : Kurosaki 7876(SHO). *Nara Pref*. Nishimura 478(TNS) : Seto 7134, 14513, Kuwashima 29760, Kodama 6694, 7018(OSA) : Watanabe 1973-1979(KOB). *Wakayama Pref*. Okamoto 7706(TI) : KANA 31669(KANA). *Tottori Pref*. Nishihara Aug. 8, 1937(TI) : MAK 107461(MAK) : Tanaka 13044, 24675(KYO) : Wada 2009, YAM 33909(YAM). *Shimane Pref*. MAK 25057(MAK) : YAM 23692, 39425(YAM). *Okuyama Pref*. Murata 27197, 27227(KYO) : Kodama 3233(OSA) : Oka 43857(YAM). *Yamaguchi Pref*. OSA 20660(OSA) : Masaki 6506, 58264 ; Oka 2912, 25102, 36531, 36608, YAM 4302, 22056, 27493(YAM). *Tokushima Pref*. Nikai 1840 ; Momiyama July 29, 1957(TI) : TNS 45963(TNS) : MAK 107460(MAK) : Murata 7745 ; Takafuji 341(KYO) : Watanabe 1980-1985(KOB) : Wada 5673(YAM). *Ehime Pref*. Oda 1608 ; Tsuyama July 26, 1934(TI) : MAK 8789, 182167(MAK) : Watanabe 1986-1991(KOB). *Kochi Pref*. TNS 303462(TNS) : Yoshinaga 5 ; Okubo 2 ; Yamanaka 49920(KYO).

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