



Evolutionary history of the Japanese flora- Cytogeographical evidences on some composites at disturbed habitats-

Watanabe, Kuniaki

(Citation)

Plant chromosome research 1987 : proceedings of the Sino-Japanese Symposium on Plant Chromosomes held at Beijing, China:25-34

(Issue Date)

1987-10

(Resource Type)

book part

(Version)

Version of Record

(URL)

<https://hdl.handle.net/20.500.14094/90001494>



EVOLUTIONARY HISTORY OF THE JAPANESE FLORA— CYTOGEOGRAPHICAL EVIDENCES
ON SOME COMPOSITES AT DISTURBED HABITATS—

Kuniaki Watanabe

Biological Institute, Faculty of General Education, Kobe University,
Kobe, 657, Japan

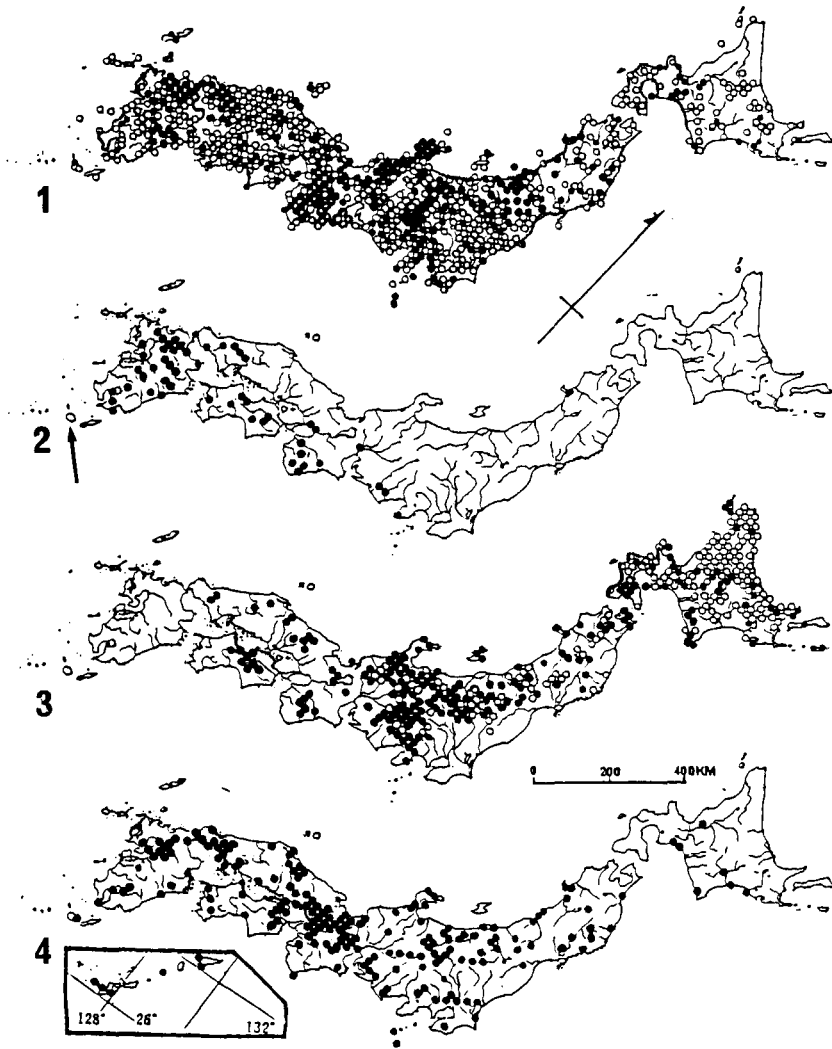
ABSTRACT

The evolutionary history of two composite genera, Eupatorium and Kalimeris, in the Japan Archipelago is interpreted on the basis of the cytogeographical data from polyploid complexes. In Eupatorium chinense var. oppositifolium which is a polyploid complex, diploids are confined to the southwestern parts of Japan which are regarded as their refuges during the last Ice Age. Agamospermous polyploids are abundant to the newly created habitats by recent human activities. Heptaploid Kalimeris yomena ($2n=7x=63$) may have been originated by the hybridization between K. indica ($2n=6x=54$) and K. incisa ($2n=8x=72$) at some stage during the last Ice Age in the southern parts of Kyushu and then has spread northward as the climate has improved. During this period, the northward range extension of both species has been accelerated by human activities, and the agamospermous polyploids of E. chinense var. oppositifolium and K. yomena with the hybrid heterosis and the ability of extensive clonal propagation have colonised preferentially into the newly available habitats. These range extensions have permitted many secondary contacts between previously separated, but still closely related species and have given rise easily to the new polyploid hybrids. The climatological fluctuations, the frequent invasions of new and superior colonizers from Eurasian continent and the Nansei Isls., the long-distant vegetational shift and the continuous supply of open habitats by human activities, during and after the Pleistocene, in the Japan Archipelago may cause the extensive hybridizations between previously separated, but still closely related species, and the subsequent polyploidizations. This may be the reason of the abundance of the neopolyploids and the successive increase of the polyploidy-levels, among perennial herbs, especially, at disturbed habitats such as forest margin, roadside and cultivated field margin, in the Japanese flora.

KEY WORDS: Eupatorium, Kalimeris, cytogeography, polyploidy, disturbance

INTRODUCTION

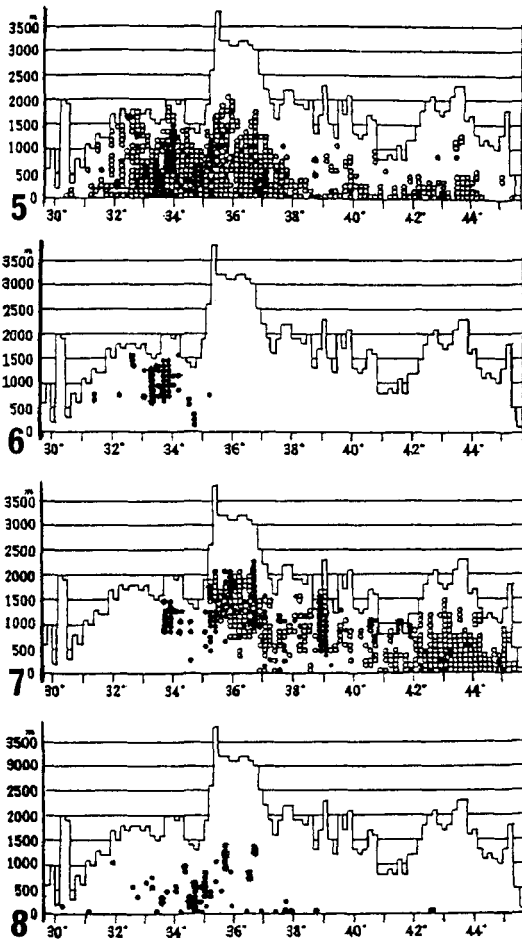
There are some features of principally asexually (either agamospermously or vegetatively) propagating species with high colonizing abilities which make them better tools for analyses of plant distribution than are principally sexually propagating species (Gustafsson, 1947; Stebbins, 1941). In the first place, the principally asexually propagating species must have arisen from sexual ancestors and can not have diverged very far from them in morphological characteristics. The identification of these ancestors should in most instances be possible by careful morphological and cytogenetical studies. If they are of allopolyploid origin, the same inferences may be drawn about past distributions of the sexual ancestors of the complex. Secondly, the relative constancy of them through many generations makes them valuable indications of ecological conditions, both in their present habitats and in past migration routes (Stebbins, 1950). Based on the same context the species or races occupied



the newly available habitats or niches created recently by human activities are the good indicators to clarify the dynamics of invasion or the recent range extension.

The Japan Archipelago is characterized by abundant rainfall and moderate temperature. Consequently, the land had been covered with forests before their destruction and there had been little chance to evolve annual colonizers. Most of existing annual colonizers may have been introduced during a recent few hundreds years and have inhabited at man-made habitats.

Eupatorium chinense var. oppositifolium is an agamosperous polyploid complex and Kalimeris yomena is the most clonally propagating species among Japanese congeners. Both species are perennials and occur mainly



Figs. 1-8. The horizontal and vertical distribution of *E. chinense* var. *oppositifolium* (1 and 5. polyploid, 2 and 6 diploid), *E. glehni* (3 and 7) and *E. lindleyanum* (4 and 8). Open circles represent the data on Horikawa's map (Horikawa, 1972, 1976); closed circles that from herbarium specimens.

on habitats created relatively recently by human activities.

This paper deals with the cytogeography of Japanese *Eupatorium* and *Kalimeris* centering around the above mentioned two species to clarify the evolutionary history of the Japanese flora, especially at disturbed habitats.

THE CYTOGEOGRAPHY OF THE GENUS EUPATORIUM IN THE JAPAN ARCHIPELAGO

(Watanabe, 1986; Watanabe and Yahara, 1984; Watanabe et al. 1982)

Six species and varieties of *Eupatorium* have been recorded in Japan. They have contiguous or overlapping geographical distribution. When their distributions are overlapped, they are ecologically isolated from each other in most cases.

Eupatorium chinense var. *oppositifolium* is widely distributed in central and northern China, Korea and Japan, and is common plants on the mountain path and the *Miscanthus* grassland. Analyses of 1024 individuals collected from 29 populations throughout the Japan Archipelago proved that this variety consisted of eight cytotypes comprising 2x, 3x, 4x and 5x based on $x=10$, and aneuploid $2n=39$, and a chromosomal deficiency. Diploids occur from the upper warm-temperate zone to the lower cool-temperate zone on the Pacific side of southwestern Japan (Figs. 2 and 6). Its habitat is confined to fragile gravitational slopes with shallow soil and rocky areas which are poor in species number and devoid of tall competitors. This small and delicate species is characterized by its slow growth and low fecundity of achenes.

On the other hand, polyploids occur abundantly and widely throughout the distributional ranges of its variety (Figs. 1 and 5). Tetraploid cytotypes were most abundant and widespread followed by triploid cytotypes in the Japan Archipelago. The frequencies of occurrence of pentaploid and the cytotypes involving a partially deficient chromosome were

relatively low. One aneuploid with $2n=39$ was found spontaneously near the northern ends of its range. All of cytotypes, except one aneuploid, were found in southwestern parts of Japan. Most of the polyploid populations exhibit various combinations of cytotypes irrespective of their temporal population size. Polyploids have tall and stout stem and can reproduce agamosperously with high fecundity. They are associated with tall grass and forb community that develops at disturbed habitats in the same climatical zone as the warm-temperate evergreen forests. Polyploids are considered less adapted to fragile gravelly slopes or rocky areas than diploids, but they are obviously superior in colonizing into the newly cleared dry habitats. The agamosperous propagation, rare sexuality and random colonization can result in the intricate mixture of various polyploid cytotypes within local populations based on their geographical backgrounds at disturbed and temporary habitats.

Eupatorium glehni has a more northbiased distribution reached to the Sachaline(RSSR)and comes in contact with E. chinense var. oppositifolium at the southern and lower marginal regions(Figs. 3 and 7). It is found in the same climatical zone with the cool-temperate deciduous forests and grows usually in mountain paths, clearings or canopy gaps. Analyses of 258 individuals collected from 13 populations throughout the Japan Archipelago proved that this species consisted of five cytotypes comprising $2x$, $3x$, $4x$ and $5x$ based on $x=10$ and an aneuploid with $2n=38$. The differences in morphology and growth habits between the diploids and polyploids of this species are less conspicuous than those of E. chinense var. oppositifolium. The abundant and widespread distribution of diploids was confirmed throughout its ranges. The occurrences of its polyploids are confined to sympatric or parapatric populations with polyploid E. chinense var. oppositifolium.

Eupatorium lindleyanum is the most widely distributed eupatoria in eastern Asia and has the similar geographical distribution with that of polyploid E. chinense var. oppositifolium in Japan(Figs. 4 and 8). It occurs in moist places such as swamps, moors, marshy grounds and follow rice fields and is ecologically separated from E. chinense var. oppositifolium occurring in drier places. Analyses of 329 individuals collected from 15 populations throughout the Japan Archipelago proved that this species consisted of five cytotypes comprising $2x$, $3x$ and $4x$ based on $x=10$ and a chromosomal deficiency. Diploids are abundant and widely distributed throughout the Japan Archipelago, except for Hokkaido Island. Most of the polyploid "E. lindleyanum" have the intermediate external morphology between diploid E. lindleyanum and polyploid E. chinense var. oppositifolium and their occurrences are scattered on the intermediate habitats adjacent to the putative parental populations. Consequently, they seem to be hybrid derivatives and to reproduce agamosperously.

During the last Ice Age the overall distribution of Japanese eupatoria appears to have withdrawn to the southwestern parts of Japan, corresponding with the southward shift of vegetation. After the last Ice Age, the overall distribution of E. glehni, E. lindleyanum and polyploid E. chinense var. oppositifolium must have extended northward and to higher elevations accompanying the climatical warming(Cf. Tsukada, 1982). In contrast, diploid E. chinense var. oppositifolium seems still to remain in the restricted areas which it had occupied during the last Ice Age. Its distribution has been restricted from the north and the higher elevations by E. glehni, from the south and the lower elevations by polyploid E. chinense var. oppositifolium and excluded from the wet habitats by E. lindleyanum. In addition, diploid E. chinense var. oppositifolium occurs on the special habitats mentioned above and is char-

acterized by the low fecundity of achene and the delicate, small and slow growth habits. It does not seem to dispossess other eupatoria invading into another habitats. Consequently, the southwestern region occupied by diploid E. chinense var. oppositifolium can be regarded as its refuge during the last Ice Age.

The southern most parts of this refuge had been isolated several times from Kyushu, as Yakushima Island (see Fig. 2 arrowed and Fig. 9), as it is as at present. Diploid Eupatorium yakuchimense endemic to this island may be differentiated from the diploid lineage of E. chinense var. oppositifolium left on this island during the earlier recurrent southward migrations.

The remaining two species, Eupatorium variabile and Eupatorium formosanum confine to the western and southern coasts of Kyushu and Shikoku, and the Nansei Isls.

Although the potential distributional range for polyploid E. chinense var. oppositifolium appears to have greatly expanded with the accompanying climatic warming, its real range extension and abundant occurrence could have been accomplished by the expansion of broken down areas from initial human activities following agricultural development and public works which took place from the southwestern and the coastal parts to the northeastern parts and the higher elevations. It may be attributed primarily to their better colonizing abilities which have resulted from luxuriant agamosperous reproduction, and rapid and tall growth habits which surpasses other competitors in the communities accompanying tall grasses and forbs. The production of most of polyploid "X E. lindleyanum" and polyploid "X E. glehni" has been accomplished by the spread or invasion of polyploid E. chinense var. oppositifolium and its hybridization with their respective diploids.

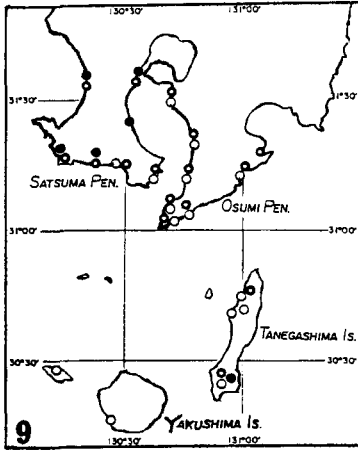
The origin of agamosperous polyploid E. chinense var. oppositifolium may be somewhere around the Yangtzu River in the central China where its variety can contact with the E. chinense var. chinense (Kawahara, personal communication). And then it has spread northward, and invade into Japan through the landbridge between Korea and Japan during the Ice Age (cf. Kaizuka and Naruse, 1977).

THE CYTOGEOGRAPHY OF THE GENUS KALIMERIS IN THE JAPAN ARCHIPELAGO (Shindo, 1964a, b, 1965, 1966a, b, 1967)

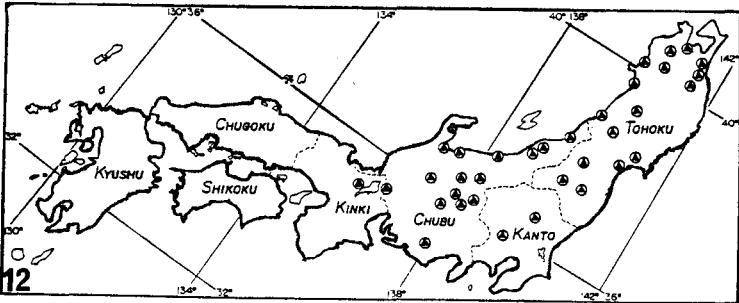
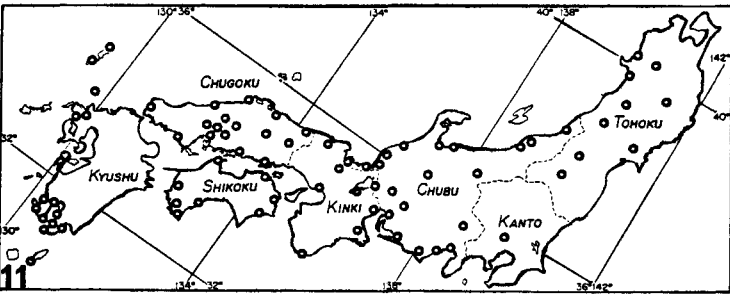
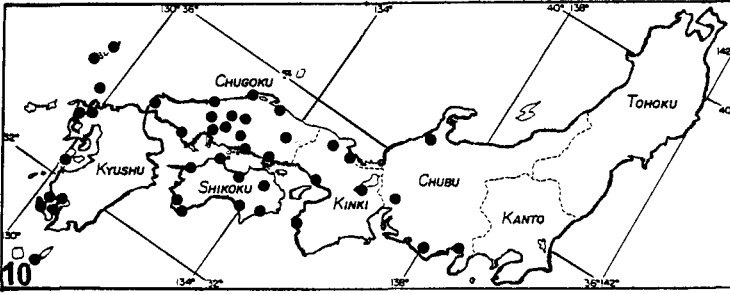
In Japan the following 4 species: K. indica (L.) Schultz Bip. ($2n=6x=54$), K. incisa DC. ($2n=8x=72$), K. pinnatifida (Maxim.) Kitamura ($2n=2x=18$) and K. yomena Kitamura ($2n=7x=63$), have been recorded (K. (=Aster) miqueliana is excluded from the genus Kalimeris in this paper based on the karyological and morphological informations). They have contiguous or overlapping geographical distribution. The latter two species are endemic to Japan.

Kalimeris indica is widely distributed in southeastern Asia and its distribution reaches to the Nansei Isls. and the southern ends of Kyushu in Japan (Fig. 9). It occurs on rich, humid, and almost bare soils around rice fields. This species hybridizes with some Aster species and gives rise to be hybrids with $2n=54$ and 72 in the Tanegashima Isl. and the Osumi Peninsula.

Kalimeris incisa has a wide distributional range over northeastern Asia: Siberia, northern China, Korea and southwestern Japan. In Japan, its distribution extends south to the Tanegashima Isl. and north and east to the coastal lowland of Ishikawa and Shizuoka Prefectures, grow-



Figs. 9-12. The horizontal distribution of Japanese *Kalimeris*. 9. The distribution of *K. indica* ($2n=6x=54$, ○), *K. yomena* ($2n=7x=63$, ◦) and *K. incisa* ($2n=8x=72$, ●) in southern Kyushu., 10. *K. incisa*, 11. *K. yomena*, 12. *K. pinnatifida* ($2n=2x=18$, ⊙).



ing on mesic or rather dry soil in weedy places by roadsides or around cultivated fields (Figs. 9 and 10). This species hybridizes with Heteropappus or Aster species and gives rise to hybrids with $2n=69-74$ in the Tsushima Isls. and the Iki Isls.

Kalimeris yomena is endemic to Japan from the Amami Isls. to Akita Pref. (Figs. 9 and 11). This species is hardly distinguishable from K. incisa by external morphology. Its principal habitats were on rich, humid soils around rice field and by roadsides and seemed to have exposed to almost continuous weeding and mowing. Its chromosome number is, mainly, $2n=7x=63$ (Table 1) and it is suspected to be hybrid derivatives between K. indica ($2n=6x=54$) and K. incisa ($2n=8x=72$) (Shimotomai and Huziwara, 1942d; Huziwara, 1958).

In the Tanegashima Isl. K. indica is more abundant than K. yomena. In the Osumi Peninsula K. yomena becomes gradually abundant towards the north, replacing K. indica by the active invasion into its habitats. In the Satsuma Peninsula the occurrences of K. indica are scattered and K. yomena becomes growing predominantly. The overlapping of geographical distribution of K. yomena and K. incisa continues from the Tanegashima Isl. to central Japan where is the northern-limits of distribution of K. incisa.

Kalimeris incisa is growing mostly on rather dry, grasscovered soils around cultivated field, fallow field and newly opened building lots, while K. yomena is growing on rich, humid soil around rice terraces. Kalimeris yomena occupies the different ecological habitat or niche from that of K. incisa. The spread of each clone of K. yomena is generally much larger than that of K. incisa. It is suggested that K. yomena can reproduce vegetatively more than K. incisa.

The distribution of K. pinnatifida (Fig. 12) overlaps with that of K. yomena from the Kansai district to Akita Pref. where the northern limits of distribution of K. yomena. Kalimeris pinnatifida and K. incisa are almost identical in ecological preference and they have contiguous geographical distribution. Accordingly the distribution of K. yomena is separated ecologically from both K. incisa and K. pinnatifida.

These ecological isolations, however, are not perfect and then they have resulted several hybrid derivatives in many localities: the aneuploid series with $2n=57-62$ in the mixed populations of K. indica and K. yomena, the aneuploid series with $2n=64-71$ in the mixed populations of K. yomena and K. incisa, the pentaploid ($2n=5x=45$) and hexaploid ($2n=6x=54$) in the mixed populations of K. yomena and K. pinnatifida.

During the last Ice Age K. incisa may have invaded into Japan through the landbridge between Korea and Japan, and come down southward. It may come to contact and hybridize with K. indica at the southern parts of Kyushu. Among these hybrid derivatives the more successful colonizers with hybrid heterosis and the ability of extensive vegetative propagation than the parental species began to migrate northward in accompany with the climatical warming after the last Ice Age. At that time there may already have been the Tsushima Strait between Japan and Korea, and then K. yomena may become to be endemic to Japan.

The northward expansion of rice field has supplied the favorite habitats for K. yomena and accelerated the expansion of distribution and the abundance of K. yomena.

The northward migration of K. indica has been prevented by the competi-

tion with the superior colonizer, *K. yomena*, having the same ecological requirements. The northward migration of *K. yomena* and *K. incisa* has been accomplished by the occupation of different habitat or niche from each other. The preferential range extension of *K. yomena* has permitted many secondary contacts between previously separated, but still closely related species and has given rise easily to new polyploid hybrids.

THE CYTOLOGICAL CHARACTERISTICS OF THE JAPANESE FLORA AT DISTURBED HABITATS

In both composite genera, *Eupatorium* and *Kalimeris*, the invasion of polyploid colonizers into Japan, the production of successful polyploid hybrids between invaders and native species, and the production and the establishment of new polyploid hybrids with highly adapted and aggressive gene combinations through the range extension and secondary contacts between previously separated but still closely related species are well in line with understanding of the Pleistocene and Postglacial history of the Japan Archipelago which suffered dramatic geological (landbridge formation between Korea and Japan, and isolation as the archipelago), climatical (cooling and warming) and vegetational (southward and northward migrations, and the supply of disturbed and open habitats by human activities) changes up to the present.

These two case-studies are instructive to explain the reason of "the abundance of neopolyploids among perennial herbs at disturbed habitats" (Ehrendorfer, 1980), such as forest margin, roadside and cultivated field margin in the Japanese flora.

Namely, the following circumstances have provided frequent opportunities for secondary contacts and hybridizations between differentiated, but still closely related species have highly adapted and aggressive gene combinations and have promoted successful polyploidy.

At first, the Japan Archipelago is located at continental arc and has been easily invaded by new superior polyploid colonizers whenever the landbridges have been constructed.

Second, new invaders can contact with native or previously separated species and produce easily polyploid hybrids, because they are still closely related.

Third, in Japan without any large seas or high mountains across the archipelago, the large scale southward-northward shift of vegetation have been permitted during the climatical fluctuations, during and after the Pleistocene, and it has supplied to give many opportunities of secondary contacts and subsequent polyploidization between different species during migrations and under sympatric conditions at the refuges.

Forth, the species richness is extremely high in Japan. Consequently, the distributions of individual species become necessarily patchy and it probably accelerates secondary contacts and subsequent polyploidizations between different species.

Fifth, the continuous supply of disturbed and open habitats during the recent 2000 years through the destruction of forest vegetation and the developments of agricultural activities from the southwest to the northeast have accelerated secondary contacts between colonizers invaded from the southwest and native species, and have given the much more chances of establishment and colonization for newly produced polyploid

hybrids. Because transient vacant or unused niches tend to be more easily created at disturbed habitats (unstable environment) than in the forests (stable environment).

The Japanese flora characterized by the species richness, the strong competitions between species and the rapid occupation of every possible niches may have only permitted the chromosomal evolution to the minor changes such as polyploidy which has maintained the preadapted genome (cf. Smith-White, 1959).

The strong correlation between polyploidy, migration and hybridization, the extreme abundance of neopolyploids at disturbed habitats and the Pleistocene-Holocene climatical history of the Japan Archipelago favour the secondary contacts hypothesis as the principal cause for successful polyploidy, as proposed by Stebbins (1984, 1985).

Table 1. Chromosome number and number of clones observed in Kalimeris yomena (after Shindo, 1967)

Number of chromosome (2n)	60	61	62	63	64	65	66	67	total
Number of clones observed	3	9	52	828	37	2	8	5	944

REFERENCES

- Ehrendorfer, F. 1980. Polyploidy and distribution. In W. H. Lewis (ed.) Polyploidy. Biological Relevance. pp.45-60. Plenum Press, New York & London.
- Gustafsson, A. 1947. Apomixis in higher plants. II. The causal aspect of apomixis. Lunds Univ. Arsskr. N. F. Avd. 2,43(2),71-178.
- Horikawa, Y. 1972. Atlas of the Japanese flora I. Gakken, Tokyo.
- Horikawa, Y. 1976. Atlas of the Japanese flora II. Gakken, Tokyo.
- Huziwara, Y. 1958. Karyotype analysis in some genera of Compositae. IV. The karyotype within genera Gymnaster, Kalimeris and Heteropappus. Cytologia 23,33-45.
- Kaizuka, K. and Naruse, H. 1977. Palaeogeographical map. In Soc. Japan Quat. Res. (ed.), The Quaternary Research in Japan. Tokyo Univ. Press. p.406.
- Shimotomai, N. and Huziwara, Y. 1942. Zytologische Untersuchungen über Aster, Gymnaster, Kalimeris und Heteropappus aus Japan. Cytologia 12,206-218.
- Shindo, K. 1964a. Cytological, morphological and geographical studies on the differentiation of species of Kalimeris in Japan I. Kalimeris indica (in Japanese with English summary). Bot. Mag. Tokyo 77:350-361.
- Shindo, K. 1964b. Cytological, morphological and geographical studies on the differentiation of species of Kalimeris in Japan II. Kalimeris pinnatifida (in Japanese with English summary). Bot. Mag. Tokyo 77:418-427.
- Shindo, K. 1965. Cytological, morphological and geographical studies on the differentiation of species of Kalimeris in Japan III. Kalimeris incisa (in Japanese with English summary). Bot. Mag. Tokyo 78:374-382.
- Shindo, K. 1966a. Cytological, morphological and geographical studies on the differentiation of species of Kalimeris in Japan IV. Geographical distribution and chromosome number of Kalimeris incisa (in Japanese with English summary). Bot. Mag. Tokyo 79:124-130.

- Shindo, K. 1966b. Cytological, morphological and geographical studies on the differentiation of species of Kalimeris in Japan V. Kalimeris yomena (in Japanese with English summary). Bot. Mag. Tokyo 79:355-365.
- Shindo, K. 1967. Cytological, morphological and geographical studies on the differentiation of species of Kalimeris in Japan. J. Sci. Hiroshima Univ. Ser. B. Div. 2 11:127-299.
- Smith-White, S. 1959. Cytological evolution in the Australian flora. Cold Spring Harbor Symp. Quant. Biol. 24:273-289.
- Stebbins, G. L. 1941. Apomixis in the angiosperms. Bot. Rev., 7,507-542.
- Stebbins, G. L. 1950. Variation and Evolution in Plants. Columbia Univ. Press, New York and London.
- Stebbins, G. L. 1984. Polyploidy and the distribution of the arctalpine flora: New evidence and a new approach. Bot. Helv. 94:1-14.
- Stebbins, G. L. 1985. Polyploidy, hybridization, and the invasion of new habitats. Ann. Mo. Bot. Gard. 72:824-832.
- Tsukada, M. 1982. Late-Quaternary shift of Fagus distribution. Bot. Mag. Tokyo 95:203-217.
- Watanabe, K. 1986. The cytogeography of the genus Eupatorium (Compositae)-A review-. Pl. Sp. Biol. 1,99-116.
- Watanabe, K., Fukuhara, T. and Huziwara, Y. 1982. Studies on the Asian eupatorias I. Eupatorium chinense var. simplicifolium from the Rokko Mountains. Bot. Mag. Tokyo 95:261-280.
- Watanabe, K., and Yahara, T. 1984. Studies on the Asian eupatoria II. Cytogeography of Eupatorium chinense subsp. sachalinense var. oppositifolium. Bot. Mag. Tokyo 97:87-105.