

Calamagrostis hakonensis (Poaceae): Distribution and Differentiation of Cytotypes

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Chromosome counts were made for a total of 540 collections of *Calamagrostis hakonensis* from 66 localities ranging from Kyushu to Hokkaido. Distribution and habitat preferences of the cytotypes involved are described. Sympatric occurrence of tetraploids (= semidiploids, $2n=28$) and higher polyploids, as well as that of septaploids and plants at hexaploid and/or octoploid levels, was confirmed in several localities, and mixtures of hexaploids and octoploids within a population were frequently observed. Plants at hexaploid and octoploid levels were the most abundant and widespread. An examination of pollen of the voucher specimens showed that tetraploids (amphimictic) had good pollen, while higher polyploids (apomictic) were generally devoid of pollen and very rarely produced moderately good pollen, the grains of higher polyploids being larger than those of tetraploids. Distributions of tetraploids and higher polyploids were more precisely delineated through an examination of pollen of many herbarium specimens. In relation to the processes by which the complicated internal structure of *C. hakonensis* has been established, the following subjects are discussed: infraspecific hybridization between ecotypically differentiated populations, enrichment of variability through occasional sexual reproduction expected in plants with more than $2n=42$, persistence of the variants by apomictic reproduction, and probable roles of some extinct taxa.

Key words: Apo-amphimictic complex — *Calamagrostis hakonensis* — Distribution of cytotypes — Infraspecific hybridization — Polyploid evolution.

Calamagrostis hakonensis Fr. et Sav. here used in the sense of Ohwi (1936, 1975) is a perennial grass which is distributed in southern areas of the Kuriles and Sakhalin, Japan and a part of China (Keng, 1959; Probatova, 1974; Ohwi, 1975). It is one of the common grass species on hills and low mountains in central and northern Japan. An enigmatic morphological variation is found in this species: some local populations are uniform, some others are polytypic, and the species is as a whole quite variable (cf. Figs. 4-8). Although most populations of *C. hakonensis* are easily separable from the other species, we sometimes encounter specimens which show close resemblance to *C. sachalinensis* Fr. Schm., *C. autumnalis* Koidz. or *C. langsдорffii* Trin. in various morphological features. In addition to the morphological diversity, extensive infraspecific polyploidy and apomictic seed formation are known to be developed in *C. hakonensis* (Tateoka, 1968, 1976). The present work aims to make clearer the internal structure of this highly variable species, which is estimated to represent an apo-amphimictic complex by itself, as a part of the systematic investigations of *Calama-*

grostis in Japan.

Chromosome counts for *C. hakonensis* have been made by Tateoka (1954, 1968, 1972, 1973, 1976). Of these five papers, four (1954, 1968, 1972, 1973) include the counts for a few collections from several mountains in Honshu, and in one (1976) are contained the counts for 195 collections from 29 localities. The lowest chromosome number detected was $2n=28$. This number manifests tetraploidy ($x=7$) in the numerical order but is estimated to be in the "semidiploid" condition, no plant with $2n=14$ chromosomes having been discovered so far (see Tateoka, 1976, for details). The other chromosome numbers detected in *C. hakonensis* were $2n=42\sim 44$ (6x level), $2n=49\sim 50$ (7x level), $2n=56\sim 58$ (8x level), $2n=63\sim 66$ (9x level), $2n=ca. 70$ (10x) and $2n=77$ (11x). The above designation such as $2n=42\sim 44$ means that different individuals with the numbers of $2n=42$, $2n=43$ and $2n=44$ were found, and one or two chromosomes smaller than the ordinary chromosomes and suggestive of supernumerary chromosomes were frequently observed in the nuclear plates showing such surplus numbers as 43 or 44. Unfortunately, it was not always possible to confirm the presence of the small chromosome in the plates showing a surplus number and to decide whether the surplus number is due to the presence of the small chromosome. Hereafter, the chromosome(s) which exist in addition to the euploid component in plants with a surplus number are collectively called the "additional chromosome".

It was first indicated by Nygren (1946) that apomictic strains of *Calamagrostis* are usually devoid of pollen in contrast to the presence of good pollen in amphimictic strains. Nygren (1946, 1954, 1958) confirmed the above attributes of the apomicts (always polyploids with more than $2n=42$ chromosomes) and the amphimicts (mostly tetraploids, viz. semidiploids, and sometimes higher polyploids) in a number of taxa of *Calamagrostis* distributed in Europe and North America. According to Tateoka (1968, 1972, 1973), plants with $2n=28$ of *C. hakonensis* had good pollen, while the strains at higher ploidy levels were devoid of pollen: the former was estimated to be amphimictic in seed formation, and the latter was assumed to have apomictic seed formation. Tateoka (1968) roughly delineated the distribution areas of these two types of *C. hakonensis* through the examination of the presence vs. absence of pollen of about one hundred herbarium specimens.

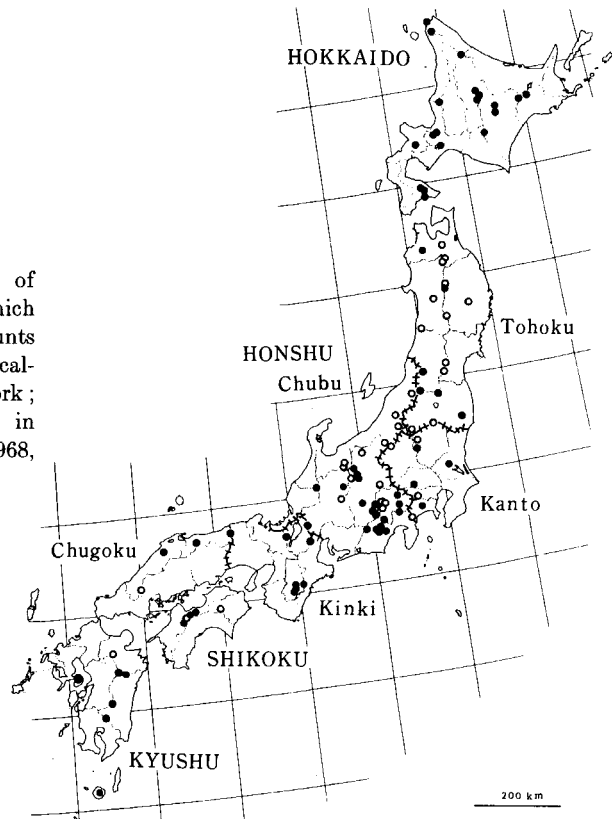
Although the cytological diversities described above have been uncovered in *C. hakonensis*, the previous chromosome counts have had apparent regional inclinations and the distributions of the cytotypes involved have been only imperfectly known. For example, no count has been made from Hokkaido and the Kinki District, and counts from Kyushu and the Chugoku District each have been confined to a few collections in one locality (cf. Fig. 1). Further, it is desirable to reexamine the pollen features of the plants at different ploidy levels on the basis of more numerous samples, since the available amount of the voucher specimens with known chromosome number was very limited at the time when the previous pollen studies were conducted. The survey of pollen features of herbarium specimens should also be done on a larger scale because the previous work (Tateoka, 1968) was founded on too few specimens to get a fair insight into the details of distribution of amphimictic and apomictic strains.

With these circumstances in mind, I have tried to make a number of new collections for the cytological survey of *C. hakonensis* so as to cover the entire range of this species in Japan and also to examine the pollen features of the voucher collections and as many herbarium specimens as possible. The results obtained are reported below, and the distribution and habitat preference of the cytotypes involved, together with some reasoning related to the processes by which the complicated internal structure of *C. hakonensis* has been established, will be presented.

Materials and Methods

Field trips for gathering the materials were made in 66 localities indicated in Fig. 1 and Table 1. Since vegetative reproduction by rhizomes occurs to a considerable extent in *Calamagrostis hakonensis*, collecting was done at intervals of appropriate distances when more than two collections were made in one locality. Root tips, fixed in Navashin's solution directly in the field, were used for chromosome observations. The plant body was prepared as a herbarium specimen at the same time. Root tips were dehydrated, embedded in paraffin and serially sectioned at a thickness of 15 μm . The crystal violet method was used for staining. The voucher specimens are enumer-

Fig. 1. Map showing the localities of *Calamagrostis hakonensis* in which materials for chromosome counts were obtained. Black circles, localities examined in the present work; white circles, those surveyed in previous works (Tateoka, 1954, 1968, 1972, 1973, 1976).



ated in Appendix 1, and they are on deposit at the National Science Museum (TNS).

Voucher specimens which were prepared during this survey and in a previous work (Tateoka, 1976), as well as the herbarium specimens, were used for pollen examination. Some of the voucher specimens were inadequate for pollen studies, and a total of 618 vouchers were observed. Herbarium specimens preserved in KYO, MAK, SAP, TI, TNS, TUS, Kanagawa Prefectural Museum and Kanazawa University, identified to be *C. hakonensis* by the present author, were used for pollen examination (the specimens used in a previous work, Tateoka 1968, were excluded). The herbarium specimens examined totalled 688. Pollen features were observed by staining pollen in a cotton blue-lactophenol solution. The grains were allowed to stain for at least 24 hr, and the grains stained deep and uniformly were scored as fertile. More than 300 grains were observed for calculating the percentage of stainable pollen. In measuring the size of pollen grains, more than ten grains per collection were examined and the mean of the measurements was adopted as the representative figure. Since the grains were typically spherical, the size was expressed by diameter.

Results

Chromosome counts

Counts for a total of 540 collections, including approximate counts for 74 collections, were made in the present work. In about 60% of the total, the numbers corresponding to the euploids on the basis of $x=7$ were obtained: $2n=28$ in 109 individuals, $2n=ca. 28$ in 3, $2n=42$ in 41, $2n=ca. 42$ in 16, $2n=49$ in 18, $2n=ca. 49$ in 2, $2n=56$ in 96, $2n=ca. 56$ in 30. In the majority of the remains, the numbers with one surplus to a euploid number were counted: $2n=29$ in 1, $2n=43$ in 123, $2n=ca. 43$ in 7, $2n=50$ in 9, $2n=ca. 50$ in 1, $2n=57$ in 60, $2n=ca. 57$ in 9. Individuals showing a surplus of two were ten in total: $2n=44$ in 3, $2n=ca. 44$ in 3, $2n=58$ in 3, $2n=ca. 58$ in 1. In one collection, a count of $2n=45$ was made. Hypo-aneuploids were scanty, and two collections showed $2n=54$ and two $2n=ca. 55$ (see Appendix 1 for the details).

As in the case of the previous work (Tateoka, 1976), a chromosome or chromosomes which were apparently smaller than the ordinary chromosomes and recalled supernumerary chromosomes were sometimes observed in the chromosome set of the collections showing the surplus numbers. Such small chromosomes could be identified in about one-fourth of the collections with the surplus number. In the rest, however, it was unclear whether the additional chromosome(s) belonged to this type of chromosomes, since the nuclear plates which were available for chromosome observations were not clear enough to allow the identification of the size and shape of individual chromosomes.

Distribution and habitats

Table 1 shows the numbers of the collections at each ploidy level divided as to localities. It also shows the distribution of the populations including the additional

Table 1. Number of collections of *Calamagrostis hakonensis* divided into ploidy levels and localities

Locality	4x level	6x level	7x level	8x level	Presence of additional chromosome ¹⁾
Kyushu :					
1. Kagoshima Pref., Mts. Miyano-uradake-Nageshidake	0	0	0	4	—
2. Kagoshima Pref., Mt. Kirishima	0	1	0	0	—
3. Kumamoto Pref., Mt. Ichifusa	0	4	0	1	+
4. Nagasaki Pref., Mt. Unzendake	0	0	0	3	—
5. Ôita Pref., Mt. Sobosan	0	2	0	2	+
6. Ôita Pref., Mt. Katamuki	0	2	0	0	+
Shikoku :					
7. Ehime Pref., Ishizuchi Range, Omogo	0	0	0	1	+
8. Ehime Pref., Mt. Kamegamori	0	0	0	7	+
9. Ehime Pref., Mts. Akaishi	0	7	0	6	+
Chugoku District :					
10. Shimane Pref., Mt. Sanbe	0	3	0	0	+
11. Tottori Pref., Mt. Daisen	0	6	0	12	+
Kinki District :					
12. Hyogo Pref., Mt. Hyonosen	0	5	0	0	+
13. Shiga Pref., Mts. Hirasano	0	8	0	0	+
14. Shiga Pref., Mt. Ibuki	0	0	0	2	+
15. Nara Pref., Mt. Sanjogatake	0	2	0	0	—
16. Nara Pref., Mt. Inamuragatake	0	4	3	0	+
17. Nara Pref., Mt. Misen	0	0	0	4	+
18. Nara Pref., Mt. Ôdaigahara	0	3	0	0	+
19. Mie Pref., Mt. Gozaisho	0	8	0	1	+
Chubu District :					
20. Ishikawa Pref., Mt. Hakusan	0	2	0	5	+
21. Gifu Pref., Kamitakaramura	0	1	0	1	+
22. Nagano Pref., Mt. Chogatake	0	0	0	1	+
23. Nagano Pref., Mt. Jônen	0	4	0	1	+
24. Nagano Pref., Ômachi, Yumata	0	2	0	1	+
25. Nagano Pref., Mt. Kiso-Komagatake, Shirabidaira	0	1	0	1	+
26. Nagano Pref., Mt. Senjogatake	0	0	0	4	+
27. Nagano Pref., Sanpuku Pass	0	0	0	1	+
28. Nagano Pref., Mt. Arakawadake	0	0	0	1	—
29. Shizuoka Pref., Misakubo	0	0	0	3	+
30. Shizuoka Pref., Sumatakyo	21	0	0	0	—
31. Shizuoka Pref., Okuizumi	6	0	0	1	—
32. Shizuoka Pref., Ikawa	22	4	0	5	+
33. Shizuoka Pref., Yokozawa	0	0	0	1	—
34. Shizuoka Pref., Umegashima	38	0	0	0	—

Table 1. Continued

	Locality	4x level	6x level	7x level	8x level	Presence of additional chromosome ¹⁾
35.	Yamanashi Pref., Mt. Fuji, Komitake	1	0	0	0	—
36.	Yamanashi Pref., Mt. Mitsutoge	15	4	0	0	+
37.	Yamanashi Pref., Mt. Kentoku	0	10	0	8	+
Kanto District :						
38.	Kanagawa Pref., Mt. Ooyama	10	0	0	0	—
39.	Saitama Pref., Mt. Izugatake	0	2	1	1	+
40.	Ibaraki Pref., Mt. Tsukuba	0	6	0	0	+
41.	Tochigi Pref., Mt. Kōshinzan	0	1	0	0	+
Tohoku District :						
42.	Fukushima Pref., Mt. Ôtake- yama	0	1	0	2	—
43.	Fukushima-Yamagata Prefs., Mts. Azuma	0	8	4	18	+
44.	Fukushima-Yamagata-Niigata Prefs., Mts. Iide	0	4	0	14	+
45.	Yamagata-Niigata Prefs., Mts. Asahi	0	2	0	25	+
46.	Akita Pref., Mt. Akita-Koma- gatake	0	4	0	9	+
47.	Aomori Pref., Mt. Iwaki	0	6	0	10	+
Hokkaido :						
48.	Hakodate, Mt. Hakodate	0	4	0	1	+
49.	Oshima, Oonuma	0	5	0	0	+
50.	Oshima, Mt. Oshima-Komagatake	0	3	0	0	+
51.	Shiribeshi, Niseko Spa	0	0	0	16	—
52.	Chitose, Shikotsu	0	7	0	0	+
53.	Ishikari, Jōzankei	0	2	0	0	+
54.	Sapporo, Mt. Moiwa	0	7	0	0	+
55.	Sorachi, Uryu	0	2	0	0	+
56.	Kamikawa, Shirogane Spa	0	6	1	6	+
57.	Kamikawa, Aizankei	0	5	4	0	+
58.	Kamikawa, 12 km northwest of Aizankei	0	0	1	0	—
59.	Kamikawa, Nyupu	0	0	15	6	+
60.	Tokachi, Nissho Pass	0	10	0	0	+
61.	Tokachi, Nukabira	0	5	1	4	+
62.	Tokachi, Horoka Spa	0	6	0	0	+
63.	Tokachi, Me-Akan	0	8	0	6	+
64.	Kushiro, O-Akan	0	2	0	4	—
65.	Soya, Toyotomi Spa	0	5	0	0	+
66.	Wakkanai	0	0	0	4	+
	Total	113	194	30	203	

¹⁾ See text as for "additional chromosome". +, present; —, absent.

chromosomes. It is apparent that (1) the tetraploids were restricted to a part of adjacent areas of Chubu and Kanto Districts on the Pacific Ocean side, (2) plants at the hexaploid and the octoploid levels were widespread throughout Japan, (3) plants at the septaploid level occurred in several geographically separated areas and were fairly common in northern and central Hokkaido, and (4) populations including the individuals with the surplus number were not restricted to a particular area but were scattered throughout Japan.

Fig. 2 shows the altitudinal distribution of the collections examined in the present work. The habitats of tetraploids greatly varied with altitude and could be divided into two sorts. (1) Habitats in other localities than Mt. Fuji: the habitats were situated in the mountain belt of the temperate zone, mostly 500–1500 m alt., and were found along roadsides or mountain paths passing through the *Quercus mongolica* var. *grosseserrata*-*Acer mono* forests or the *Pinus densiflora*-deciduous broad leaf forests. (2) Habitat on Mt. Fuji, a young volcano covered by recent lava: the habitat was located on lava soils at the vicinity of Komitake (2350 m alt.) where the subalpine conifer forest was contiguous to the volcanic barrens. It must be noted that, though a count of $2n=28$ was made for only one individual in this population, the population could be regarded to be principally tetraploid and might have been existing for a long time since several old herbarium specimens collected at the vicinity of Komitake which were estimated to be tetraploids by their pollen features have been discovered (vide infra).

The habitats of plants at the hexaploid level and those at the octoploid level were quite diverse. The habitats were mostly mesic, sometimes on dry stony ridges or on poorly drained soils in the shade, and not scarce on volcanic soils. As shown in Fig. 2, these plants were located in high altitudes of southwestern Japan, in a variety of sites from low hills to high mountains in central and northern Honshu, and in many sites on foothills and mountainsides in Hokkaido. An apparent difference between plants at the hexaploid level and those at the octoploid level was that the octoploid plants were more abundant than the hexaploid plants in the alpine habitats over 2000 m alt. Plants at the hexaploid level were not detected in the alpine habitats in the present work, though a few were located at high altitudes over 2000 m on the Akaishi Range in previous works (Tateoka, 1972, 1976). The majority of plants at the septaploid level were sympatrically growing with hexaploids and/or octoploids, and no preference for a particular environmental condition was obvious in the septaploid plants.

Population structure in relation to polyploidy

It can be seen from Table 1 that mixtures of plants at different ploidy levels were confirmed in 29 of the 66 local populations examined. Plants at the same ploidy level only were found in each of the other 37 populations.

Populations without mixtures. Although no mixture was found in the 37 populations, it is apparent that a homoploid condition can not be asserted for the populations in which only one or a few individuals were used for chromosome counts unless the

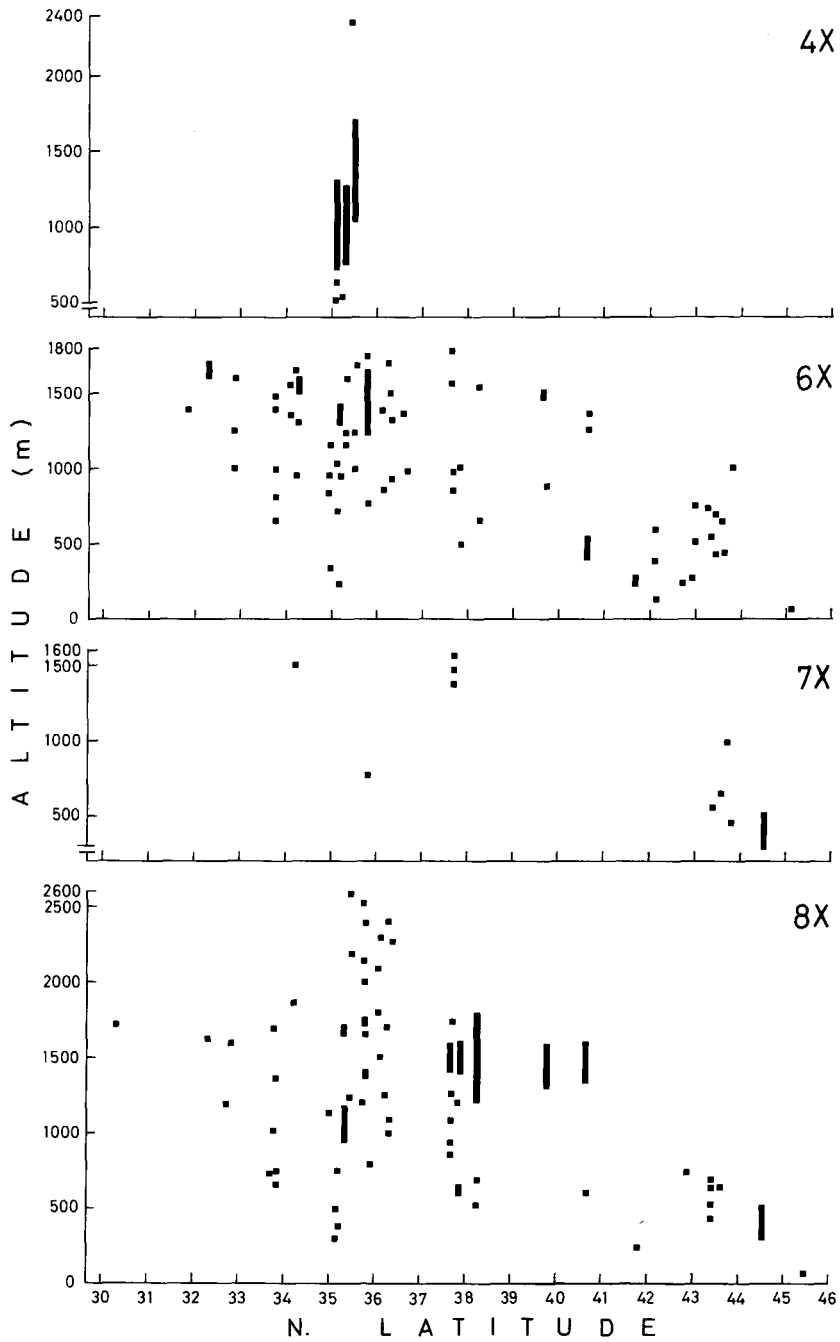


Fig. 2. Altitudinal distribution against latitudes of the collections of *Calamagrostis hakonensis*, divided into ploidy levels.

population concerned was very small, and that due caution should be exercised for estimating a homoploid structure even for the populations in which the same chromosome number was detected in a considerable number of samples. Taking the populations in which more than ten individuals were cytologically examined, only five were stable in the ploidy level. Three of the five populations were tetraploid (Loc. 30, 34, 38), one hexaploid (Loc. 60), and one octoploid (Loc. 51). It was remarkable that counts of $2n=56$ were invariably made for 16 individuals randomly collected from the population at Loc. 51, which developed along roadsides on shrubby mountain slopes stretching for about 800 m.

Mixtures of tetraploids and higher polyploids. So far as examined, three populations belonged to this category. A mixture of plants at the tetraploid and the hexaploid levels was found at Mt. Mitsutoge (Loc. 36), in which tetraploids grew sporadically along a mountain path leading to the summit and hexaploid plants occurred sparsely along with the tetraploids (see Fig. 3a). These plants were very similar morphologically, as in the case of the sympatric tetraploids and hexaploids at Ikawa appearing in Fig. 4. In the population at Okuizumi (Loc. 31), an octoploid was found surrounded by tetraploids, and the octoploid and the tetraploids were again very similar morphologically. In the population at Ikawa (Loc. 32), both hexaploids and

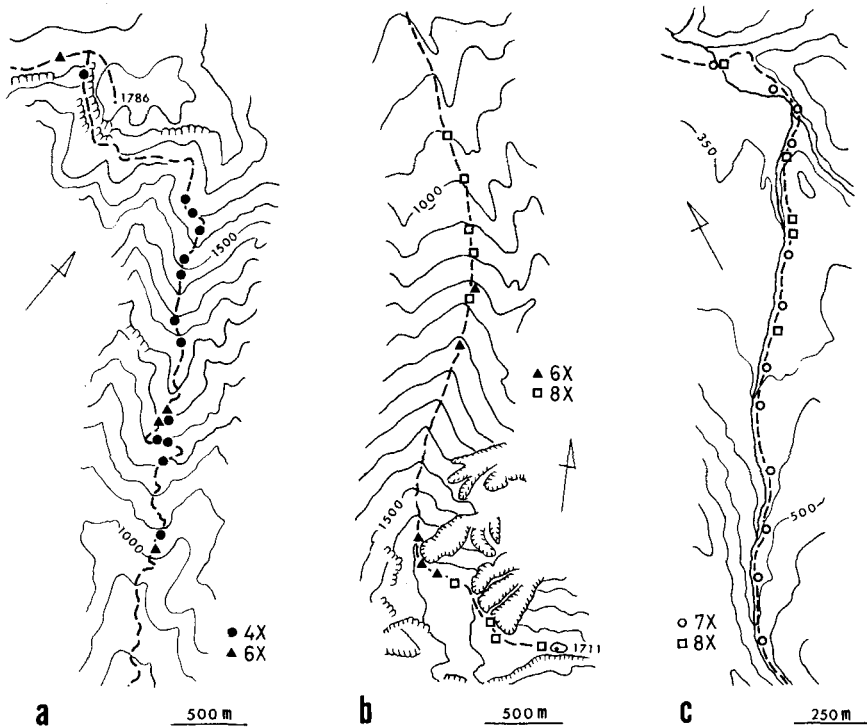


Fig. 3. Maps showing the sites of the collections of *Calamagrostis hakonensis* in three localities. Contour intervals are 50 m. a: Mt. Mitsutoge (Loc. 36). b: Mt. Daisen (Loc. 11). c: Nyupu (Loc. 59). Some collections with additional chromosomes (see text) are included in 6x, 7x and 8x (see Appendix 1 for details).

octoploids grew sympatrically with tetraploids which apparently represented the dominant component of this population. No clear-cut morphological differences were noticed among these plants, though spikelets of the octoploids were generally somewhat larger than those of the others. Tetraploids in these different populations were similar in appearance.

Mixtures of plants at the hexaploid and the octoploid levels. This type of mixture was the most frequent and was found in 19 of the 66 populations examined. The mixed conditions within a local population included the cases that (1) plants at the hexaploid and the octoploid levels were detected in different colonies which were more or less separated, and (2) the two types of plants were found not only in different colonies as above but also in one and the same colony. The former case was found in 13 of the 19 relevant populations, and the latter was encountered in six populations. An example of the latter case is illustrated in Fig. 3b. Morphological variability of the populations belonging to this category was multiform: plants at the hexaploid and the octoploid levels were very similar in some populations and different in some others, and the variability of plants at the same ploidy level within a population was likewise small or large according to populations. Some plants at either hexaploid or octoploid levels were extremely deviated from the tetraploids morphologically. Two examples are shown in Figs. 5 and 6. Plants indicated in Fig. 7 (6x-8x) can also be cited as one of the forms extremely deviated from the tetraploids.

Populations including plants at the septaploid level. Plants at the septaploid level were detected in eight populations. When the presence of additional chromosomes is disregarded, the populations can be expressed as follows: $6x + 7x8x$ in four, $6x + 7x$ in two, $7x + 8x$ in one, $7x$ only in one. The last (Loc. 58) is the population in which only one individual was cytologically examined, and it was ambiguous as to whether this population lacked a mixture of different cytotypes. In the other populations, plants at the septaploid level grew in proximity to hexaploid and/or octoploid plants (see Fig. 3c). In morphological features, the septaploid plants were generally close to hexaploid and/or octoploid plants sympatrically growing in respective populations. Examples are shown in Figs. 7 and 8. It is evident that the septaploid collection from Mts. Azuma (Loc. 43) indicated in Fig. 7b was closer to the hexaploid and the octoploid plants from the same population (Figs. 7a, c) than to the septaploid from Nyupu (Loc. 59) indicated in Fig. 8a, and the Nyupu septaploid was in turn very close to the octoploid from the same population appearing in Fig. 8b. As is clear in Table 1, the observed frequencies of plants at the septaploid level were minor in most of the populations including them, but the plants were apparently predominant in the population at Nyupu (see Fig. 3c). The Nyupu population, in which no hexaploid was found, was rather stable in morphological features, and some matured seeds were observed in a few septaploids from this population.

Examination of pollen

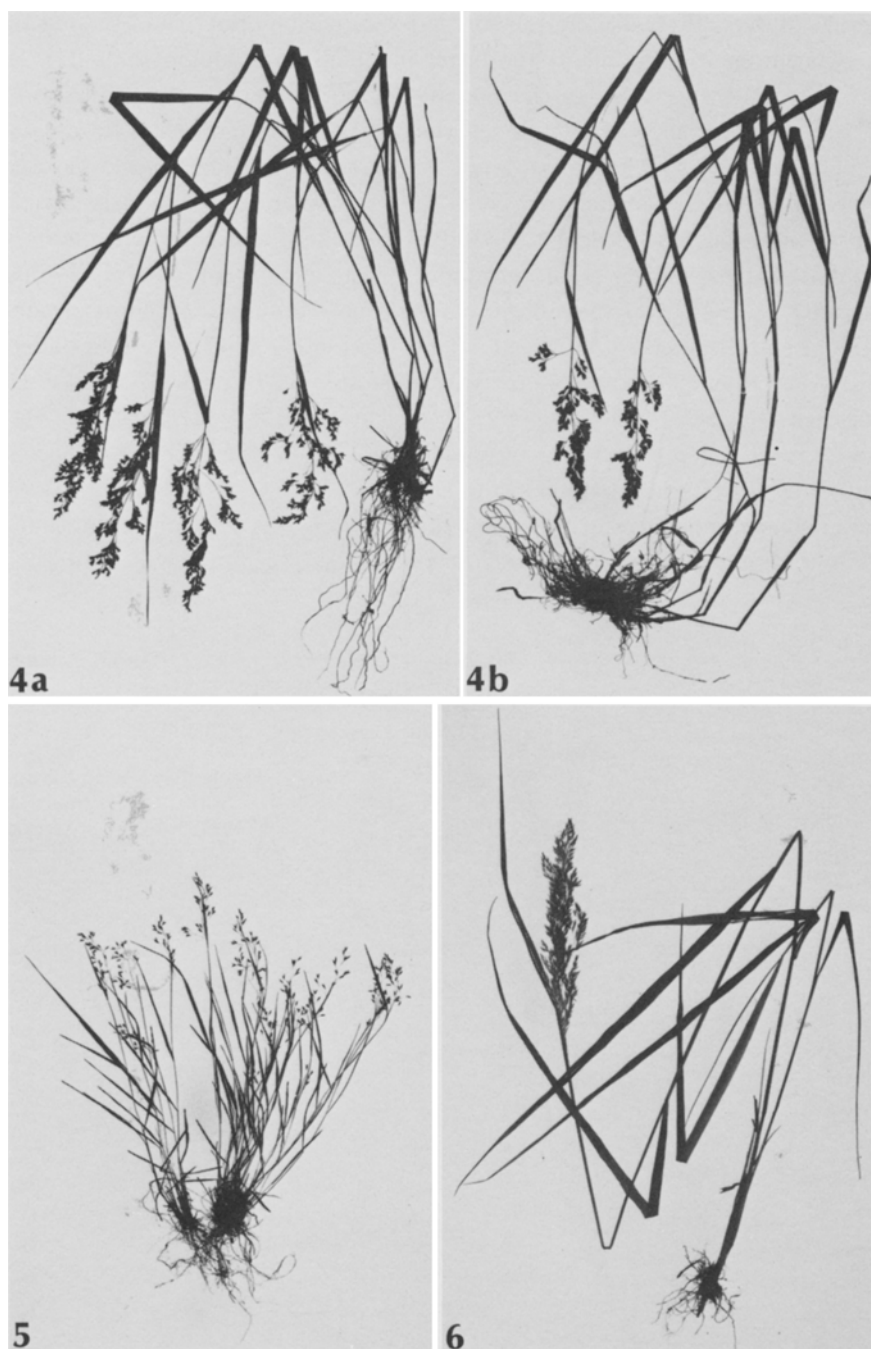
As stated earlier, not only the collections appearing in Table 1 and Appendix 1 but also the collections whose chromosome numbers were reported in a previous paper

(Tateoka, 1976) were used as materials for the examination of pollen of the individuals with known chromosome number (the latter included some plants at 9x-11x levels). Results of the observations as to the presence of pollen and its stainability of these voucher specimens are shown in Table 2. Good pollen with more than 70% stainability was found in almost all the tetraploids, and in two collections the stainability was somewhat lower but still moderately good. On the other hand, the large majority of the collections at the 6x-11x levels, including hexaploid and octoploid plants which were sympatrically growing with tetraploids, were devoid of pollen. Pollen was found in only 11 (2.1%) of the collections with more than $2n=42$ chromosomes, and in 7 of the 11 collections the grains were almost completely abortive. Bad pollen with stainability less than 20% was detected in one hexaploid (*Tateoka 16387*, Loc. 15) and two octoploids (*Tateoka 9491*, Mt. Tsurugi, cf. Tateoka 1976; *17222*, Loc. 44), while moderately good pollen was found in one octoploid collection (*Tateoka 18530*) from Me-Akan (Loc. 63) (stainability 60.2%).

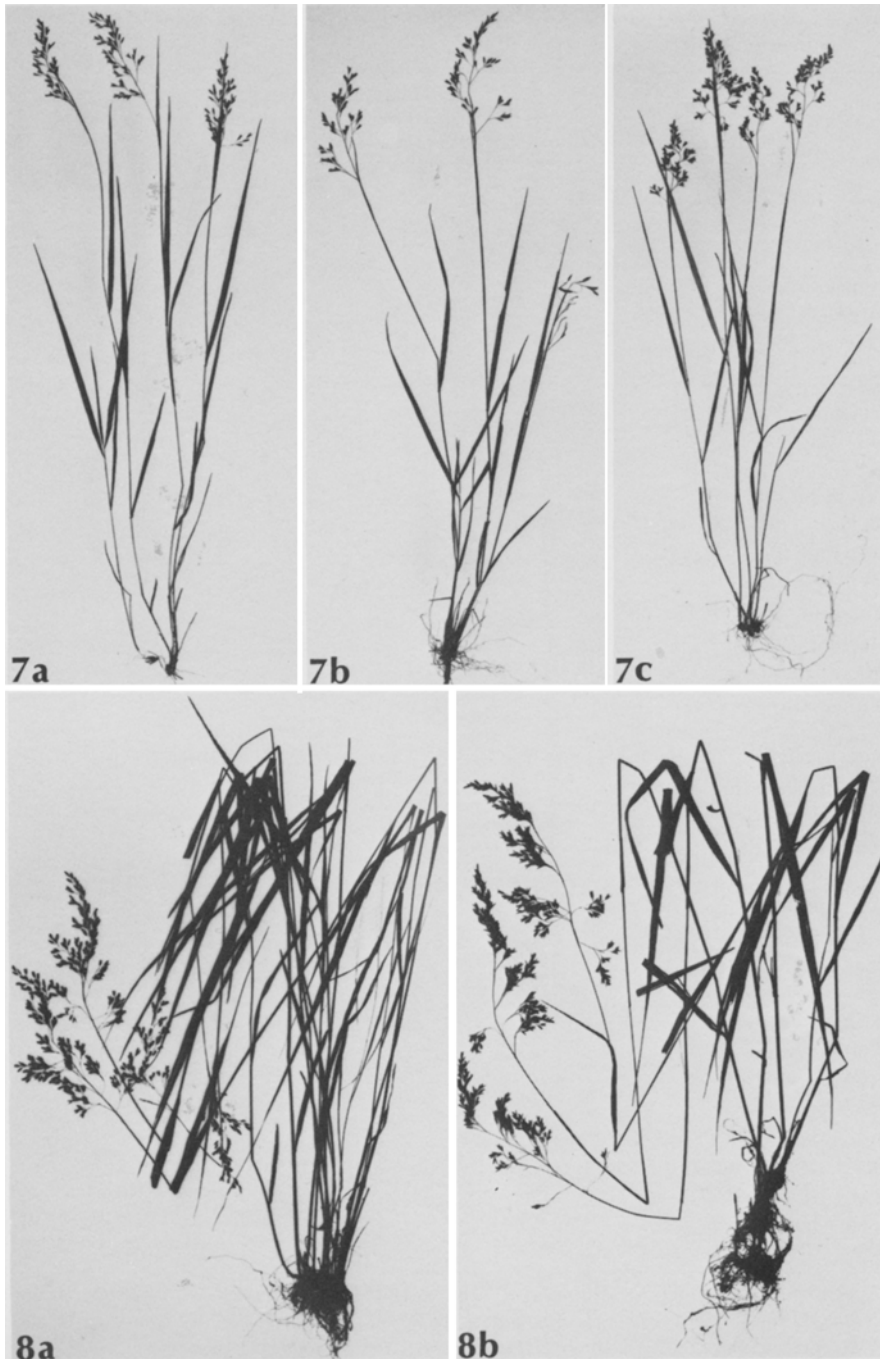
One of the consequences of the above observations was that a combination of the presence and stainability of pollen was insufficient as a criterion which discriminates

Table 2. Number of specimens of *Calamagrostis hakonensis* showing respective pollen features

	Pollen absent	Pollen present (% stainable pollen)			
		very bad (0% or nearly 0%)	bad (2-20%)	moderately good (40-70%)	good (more than 70%)
Voucher specimens :					
4x level	0	0	0	2	82
6x level	225	0	1	0	0
7x level	30	0	0	0	0
8x level	254	6	2	1	0
9x level	13	0	0	0	0
10x level	1	0	0	0	0
11x level	0	1	0	0	0
Total	523	7	3	3	82
Herbarium specimens :					
Kyushu	42	2	0	0	0
Shikoku	28	0	0	0	0
Chugoku District	21	0	0	0	0
Kinki District	45	0	0	0	0
Chubu District	174	3	0	1	17
Kanto District	104	2	0	0	12
Tohoku District	126	3	0	0	0
Hokkaido	102	1	0	0	0
Southern Kuriles	5	0	0	0	0
Total	647	11	0	1	29



Figs. 4-6. *Calamagrostis hakonensis*. $\times 0.22$. 4a: *Tateoka 19027*, $2n=28$, from Ikawa (Loc. 32). 4b: *Tateoka 19049*, $2n=42$, from Ikawa. 5: *Tateoka 16387*, $2n=42$, from a rocky habitat at Mt. Sanjogatake (Loc. 15). 6: *Tateoka 16314*, $2n=ca. 56$, from Mt. Kamegamori (Loc. 8).



Figs. 7 and 8. *Calamagrostis hakonensis*. $\times 0.22$. 7: collections from Ubayu-Yakushimori, Mts. Azuma (Loc. 43). 7a, *Tateoka* 17407, $2n=42$; 7b, 17405, $2n=50$; 7c, 17392, $2n=56$. 8: collections from Nyupu (Loc. 59). 8a, *Tateoka* 19369, $2n=50$; 8b, 19366, $2n=ca. 57$.

Table 3. Number of specimens of *Calamagrostis hakonensis* showing respective diameter of pollen grains

	Diameter of pollen grains (μm)												
	27 —	28 —	29 —	30 —	31 —	32 —	33 —	34 —	35 —	36 —	37 —	38 —	39
4x		3	2	3	8	4	4	1					
6x										1			
8x										2		1	
Specimens from the localities in question ¹⁾ :													
1. Nagano Pref., Kizawa				1									
2. Nagano Pref., Ikuta					1								
3. Shizuoka Pref., Mt. Tenshi		1				1							
4. Shizuoka Pref., Mt. Ashitaka		1				1							
5. Shizuoka Pref., Mt. Fuji, Fujinomiya					1								
6. Shizuoka Pref., Mt. Fuji, Tarôbo						1							
7. Shizuoka Pref., Mt. Fuji, Suyama			1										
8. Yamanashi Pref., Mt. Fuji, near Komitake				1	1								
9. Yamanashi Pref., Mt. Howo, Norogawa						1							
10. Yamanashi Pref., Mt. Kinpuzan		1											
11. Yamanashi Pref., Mt. Kentoku					1								
12. Kanagawa Pref., Mt. Mikuni							1						
13. Kanagawa Pref., Tanzawa, Hookizawa					1								
14. Kanagawa Pref., Mt. Oomuro						1							
15. Kanagawa Pref., Mt. Hinokiboramaru						1							
16. Tokyo Pref., Tama Hills, Yaen Pass				1									

¹⁾ Specimens examined. 1, *Muramatsu* 1948-VII-17. 2, *Sugimoto* 1925-VIII-4. 3, *Kadota* 2543, 3534. 4, *Ohba* 1951-VII-30, *Kanai* 6902. 5, *Murata* 37190. 6, *Konta & Matsumoto* 102. 7, *Wakana* 1969-VI-15. 8, *Ishizuka* 84, *Nakai* 2888. 9, *Okamoto* 1963-VIII-9. 10, *H. Koidzumi* 54023. 11, *Tateoka* 17152. 12, *Mori* 1982-VII-28. 13, *Katsuyama* 1982-VI-27. 14, *Katsuyama* 1982-VII-28. 15, *Nishio* 1959-VII-24. 16, *Tateoka* 1950-VII-3.

sconsistently between tetraploids and higher polyploids, because moderately good pollen was found in both two tetraploids and one octoploid. Differences in pollen size were therefore examined on the basis of 25 tetraploids with good or moderately good pollen, one hexaploid with bad pollen and three octoploids with bad or moderately good pollen. The results of the measurements of pollen diameter of these collections are indicated in Table 3. In the tetraploids the grains were 27–34 μm in diameter, while they were significantly larger (more than 35 μm) in the higher polyploids. These results show that tetraploids and higher polyploids of *Calamagrostis hakonensis* can be separated by pollen features with a higher degree of certainty when the size of

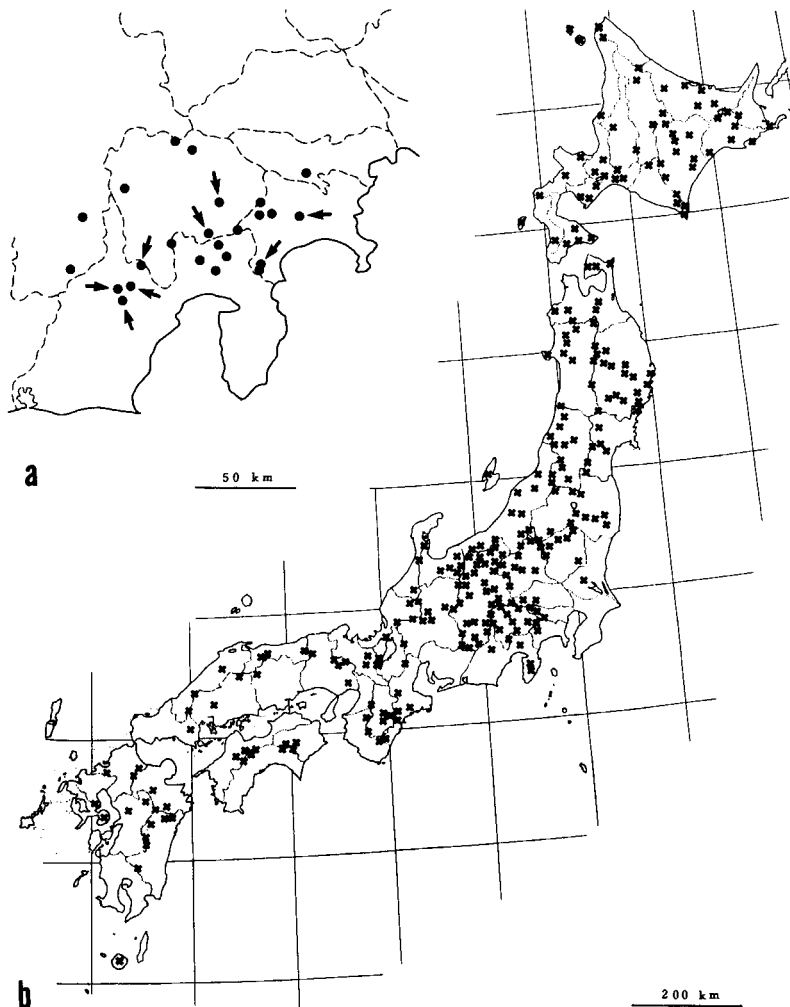


Fig. 9. Localities of *Calamagrostis hakonensis* in Japan. a: Localities of the specimens with good pollen, estimated to be tetraploid ($2n=28$). Arrows have been attached to the localities where the occurrence of tetraploids was confirmed by chromosome counts. b: Localities of the specimens which were devoid of pollen or showed abortive pollen, estimated to be higher polyploids with more than $2n=42$ chromosomes.

the grains is taken into account.

A survey of pollen features of the herbarium specimens was carried out with an aim of ascertaining the distribution areas of tetraploids and higher polyploids on the basis of the above criteria. As shown in Table 2, specimens with good or moderately good pollen were confined to 30 specimens obtained from Chubu and Kanto Districts. Localities of the 30 specimens were divided to (1) the localities where the occurrence of tetraploids was confirmed by chromosome counts, and (2) the localities in which the distribution of tetraploids was unknown. Pollen size of these specimens was subjected to examination, and the results obtained in 17 specimens from the localities of (2) and two specimens from the vicinity of Komitake on Mt. Fuji are shown in Table 3. It is clear that all the 19 specimens were situated within the range of tetraploids in pollen size. It may therefore be justified to regard these specimens to be tetraploid. The specimens from the localities of (1) other than Komitake were likewise ascribed to tetraploids by the same token. The distribution maps of the specimens thus identified to be a tetraploid or higher polyploids are shown in Fig. 9. It is evident that the maps obtained were in agreement with the expectations derived from the results of chromosome counts and that a somewhat wider range of tetraploids was confirmed. Most of the sites of tetraploids newly uncovered by the survey of herbarium specimens were situated at the montane belts judging from their geographies and notes on labels of the specimens.

Discussion

Fig. 10 shows the distribution of plants at different ploidy levels thus far uncovered in *Calamagrostis hakonensis* on the basis of the present and previous chromosome counts (Tateoka, 1954, 1968, 1972, 1973, 1976). In a previous paper (Tateoka, 1976) was reported the occurrence of a population including a number of plants at the enneaploid level ($2n=63\sim66$) on a slope near the summit of Mt. Zawo, one collection with $2n=ca. 70$ (10x) from Hachimantai, and one with $2n=77$ (11x) from Mt. Zawo. In the light of the present work, it has become evident that these high polyploids are quite rare in *C. hakonensis* of Japan. The main body of this species in Japan is undoubtedly composed of plants at the hexaploid and the octoploid levels which are equally widespread. It is now clear that the geographical range of tetraploids is restricted to the realm indicated in Fig. 9a. According to my field experience, the area with abundant occurrence of tetraploids roughly corresponds to the inside of the line enclosure that is made up by connecting the localities accompanied by an arrow in Fig. 9a, and the tetraploids are less abundant in more peripheral localities. Some peripheral tetraploid populations, such as a population at Yaen Pass, seem to have already faded away to extinction owing to recent human destruction.

Because no chromosome count has been made for *C. hakonensis* distributed outside Japan, it is obscure what cytotypes occur there. However, it is most probable that the strains of this species growing in southern Kuriles and Sakhalin are hexaploids and octoploids. As shown in Table 2, the five specimens from southern Kuriles lacked

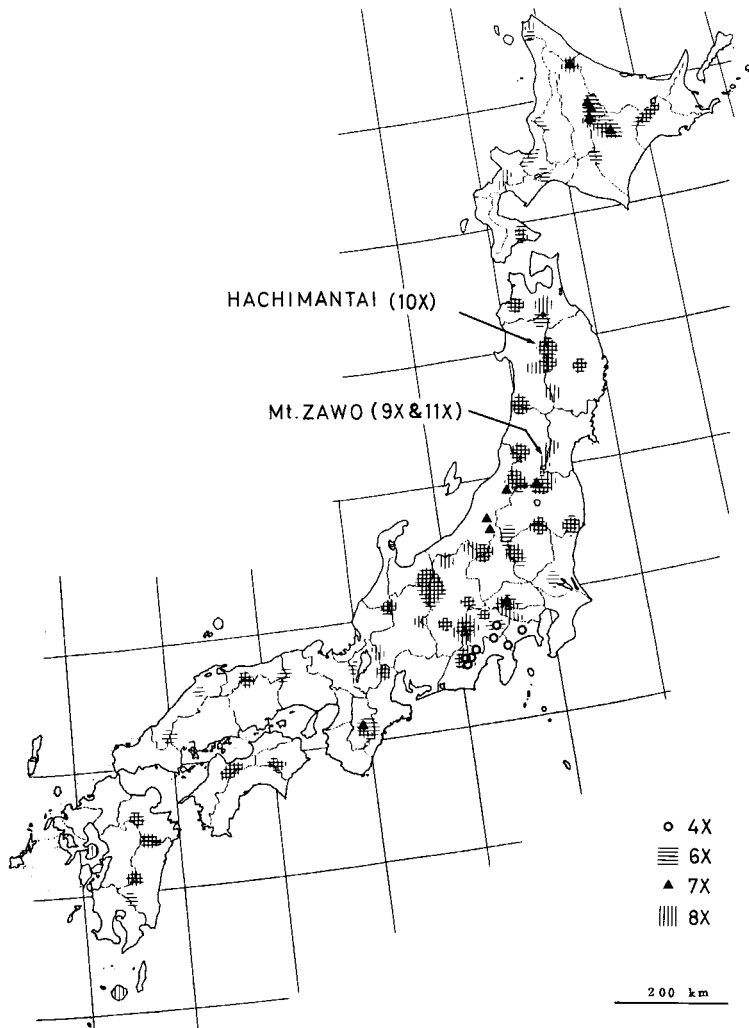


Fig. 10. Distribution of cytotypes of *Calamagrostis hakonensis* in Japan.

pollen. The occurrence of the tetraploids in China would be possible, but it is difficult to confirm this possibility at the present time.

Some reasoning related to the processes by which the complicated internal structure of *C. hakonensis* has been established can be done based on the results of the present survey. First, ecotypic differentiation at the tetraploid (=semidiploid) level and its significance in polyploid evolution should be pointed out. The habitat of the tetraploid population detected near Komitake on Mt. Fuji must be conspicuously different edaphically and climatically from the habitats on the lower mountain belts where most of the tetraploid populations were located. The sites of the tetraploids previously reported (Tateoka, 1954, 1976) from Mts. Hakone, which are close to Mt. Fuji, were situated on sulphureous volcanic soils at the altitudes of 780–1400 m. The

habitats on Mts. Hakone were edaphically closer to the habitat on Mt. Fuji and climatically more similar to the habitats at the mountain belts which were surveyed in the present work. The tetraploid populations occurring in these contrasting environments must have different ranges of ecological tolerance, and it is very likely that such ecotypic differentiation has proceeded from ancient times in response to historical vicissitudes of the edaphic and climatic conditions in the southern part of the adjoining region of Kanto and Chubu Districts which must have been greatly influenced by volcanic activities in the Fuji-Hakone volcanic zone.

The importance of crossing between differently adapted populations within a species (=intraspecific hybridization) in successful polyploid evolution has recently been stressed by Stebbins (1980). In such a plant group as *Calamagrostis* which includes many species having intraspecific polyploidy, intraspecific hybridization that enables polyploid derivatives to escape from adaptive inferiority associated with autopolyploidy seems to have particular significance. In *C. hakonensis*, intraspecific hybridization leading to successful polyploid evolution can be expected in two alternative ways. One of them is the hybridization between tetraploids followed by polyploidization, and another is hybridization between raw autopolyploids which are produced by polyploidization antecedent to hybridization (sexual reproduction in plants with more than $2n=42$ chromosomes may be minor, but it can not be estimated to be nil as discussed later). In this context, notice should be given to plants at the hexaploid and the octoploid levels which were found within a population dominated by tetraploids and closely resembled the surrounding tetraploids in morphological features. It may be justifiable to suppose that these hexaploid plants have arisen through the union of an unreduced gamete and a reduced gamete of sympatric tetraploids and exist as raw autopolyploids. The origin of hexaploids of this nature is known in a few other species of *Calamagrostis* (Tateoka, 1976 and unpub.), as well as in various other plant groups (Týrl, 1969; Estes, 1969; Stuessy *et al.*, 1973; Harlan and de Wet, 1975; de Wet, 1980; Stutz and Sanderson, 1983). The origin of the above mentioned octoploids through the union of an unreduced gamete of the hexaploid as above and a reduced gamete of the original tetraploid would be somewhat more dubious, but the assumption that these octoploids (=semitetraploids) may be raw autopolyploids is supported by their close resemblance to the sympatric tetraploids in morphology and ecology. It is entirely possible that hexaploids and octoploids of *C. hakonensis* have arisen as raw autopolyploids several times in different tetraploid populations having different adaptive norms. Intraspecific hybridization may have been possible not only between tetraploids but also between these raw autopolyploids, and sometimes between tetraploids and raw autopolyploids. It is likely that most of the plants at the hexaploid and the octoploid levels now widespread as the main components of *C. hakonensis* have become successful by virtue of intraspecific hybridization as discussed above.

Secondly, it can be pointed out that sexual reproduction in plants with more than $2n=42$ chromosomes should be admitted at any rate, though Tateoka's earlier works (1968, 1972, 1973) showed the complete absence of pollen in all the examined collec-

tions of this species with more than $2n=42$ and a similar result was obtained in the present work. Among the collections with more than $2n=42$ of which pollen was here examined, the collections producing pollen were only 2.1% and those showing fairly good pollen were 0.19% (Table 2). The percentage of 0.19 is very small in itself, but it is quite meaningful when the enormous number of individuals of *C. hakonensis* actually growing in nature is considered. The occurrence of a considerable amount of sexual reproduction is suggested, and crossing is expected between those plants with functional gametes, as well as between such plants of *C. hakonensis* and some other related species; *Calamagrostis* is mainly allogamous, and interspecific hybridization is common in this genus (Nygren, 1946, 1962).

Whatever the rate of crossing of the polyploids of *C. hakonensis* is, the consequence of the chromosome survey appearing in Table 1 and Fig. 10 can not logically be explained without assuming crossing between plants at the hexaploid and the octoploid levels. Plants at the septaploid level must have been produced through $6x \times 8x$, because in the present case other possibilities, such as $4x \times 10x$, can be ruled out. The septaploid plants detected in various localities seem to have arisen *in situ*, considering the facts that (1) some of the localities were far distant geographically and (2) septaploid plants in respective localities were generally closer to hexaploids and/or octoploids sympatrically growing within the same area than to septaploid plants in other localities in morphological features. This view conforms with the fact that plants at the hexaploid and the octoploid levels were often sympatric within the same population. Sporadic occurrences of the $10x$ and the $11x$ plants, which would be only ephemeral, can also most reasonably be understood when the unions of reduced and unreduced gametes of hexaploids and octoploids are postulated. The enneaploid plants may have been produced by either the union of reduced and unreduced gametes of hexaploids or, more likely, the union of an unreduced gamete of the septaploids and a reduced gamete of some other tetraploid species of *Calamagrostis* growing on Mt. Zawo.

Thirdly, it is indicated by different frequencies of septaploid plants in several populations including them that the products of occasional sexual reproduction may sometimes be extant only as ephemeral beings and may at times develop into biotypes which dominate in large or small areas by aid of apomictic reproduction. In most of such populations, plants at the septaploid level were minor. However, in the population at Nyupu (Loc. 59) which stretched out over 1 km (Fig. 3c), septaploid plants were apparently dominant and seemed to have acquired the present range by vegetative reproduction and through the dispersal by seeds apomictically formed. Some matured seeds were actually found in a few septaploids of this population, and the hexaploid plant which is one of the putative parents seemed to have already disappeared or diminished in this population. A similar state of affairs may be prevailing in plants at the hexaploid and the octoploid levels; without doubt apomictic seed formation is usual in these plants (Tateoka, 1968, 1973). Thus, the production of new recombinants by occasional sexual reproduction and the maintenance of the variants by apomictic reproduction may be prevailing in strains with more than $2n=42$ chromo-

somes of *Calamagrostis hakonensis* and may be largely responsible for their variability. This is a situation which is well known in various examples of the apo-amphimictic species or species complexes (Gustafsson, 1946-1947; Stebbins, 1950; Grant, 1981).

Finally, it seems almost certain that some extant or extinct tetraploids other than the tetraploids of *C. hakonensis* have participated in the genesis of plants with more than $2n=42$ chromosomes which are included within the limit of *C. hakonensis* as presently interpreted but are extremely deviated morphologically from the representative type of *C. hakonensis* (the representative type designates the type which is most commonly found and similar to the extant tetraploids morphologically, cf. Figs. 4 and 8). For example, when plants at the hexa-, septa- and octoploid levels detected at Mts. Azuma (Figs. 7a-c) are compared with the tetraploids (Fig. 4a), one would even guess that they may belong to different species; it is hardly imaginable that the tetraploids are the ancestor of the higher polyploids growing on Mts. Azuma. Although these two types are morphologically connected by some intermediates, it is very unlikely that both hexaploids and octoploids of the Mts. Azuma type have evolved in parallel from hexaploids and octoploids of the representative type through the processes of mutation, recombination and selection. Another point which should be stressed is that the origin of the octoploids of the Mts. Azuma type can be reasonably understood only when the participation of an extinct (or still undetected) tetraploid taxon which is different from the extant tetraploids and closer to the Mts. Azuma type is postulated, because the derivation of octoploids from hexaploids only is very unlikely. The most likely hypothesis regarding the genesis of plants of the Mts. Azuma type and their connection with the representative type of *C. hakonensis* may be as follows: the higher polyploids of the Mts. Azuma type have been derived from extinct tetraploids of this type independently of the extant tetraploids, and the higher polyploids of the Mts. Azuma type and the representative type have been connected via hybridization which has given rise to some intermediates obscuring the boundary between the two originally disparate groups. Many more studies are needed to clarify the details of the matters as above which can be visualized from the results of the present work regarding the complicated internal structure of *C. hakonensis*, and such studies are now in progress.

I am grateful to Mr. Muneo Michikawa, the University of Tsukuba, who kindly helped me in field explorations and supplied some materials for the chromosome counts. This work was supported by the Grant-in-Aid for Scientific Research, No. 548013, and the Grant-in-Aid for Special Project Research, No. 58124034, from the Ministry of Education, Science and Culture of Japan.

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Appendix 1. Enumeration of voucher specimens

Locality numbers correspond to those appearing in Table 1. Chromosome numbers (2n) are indicated by boldface, and collection numbers in italics. The collection numbers without an alphabetic symbol are the author's, and those with *M* are collections by Muneo Michikawa. When relevant collection numbers are continuous, the initial number and the final figure of the last number are connected by a wave line: e.g., *14312*~*3* designating two collections with the numbers *14312* and *14313*. The following denotations are used in the case that one or a few additional chromosomes (cf. text) exist: when the additional chromosome(s) are apparently smaller than the ordinary chromosomes and suggestive of supernumerary chromosomes, the designation accompanied by a plus sign is given, e.g., **42+1**; when it is uncertain whether the additional chromosome(s) are ordinary chromosomes or putative supernumeraries, only the chromosome number is given, e.g., **43**.

Kyushu. 1. Kagoshima Pref., Isl. Yakushima, Mts. Nageshidake-Miyanouradake, 1700-1750 m, 14312~3, 56; 14297, 14302, ca. 56. — 2. Do., Mt. Kirishima, near Tarô Pond, 1400 m, 19528, ca. 42. — 3. Kumamoto Pref., Mt. Ichifusa, summit area, 1600-1700 m, 19535, 19562, 42; 19532, ca. 42; 19536, 43; 19563, 56. — 4. Nagasaki Pref., Mt. Unzen, Hatoana, 1200 m, 19633~5, 56. — 5. Ōita Pref., Mt. Sobosan, 1000 m, 14366, 43; 1500-1700 m, 14374, 43; 14379, 56; 14373, ca. 56. — 5. Do., Mt. Katamukiyama, Tsuzurage, 1250-1280 m, 16734, 16736, 43.

Shikoku. 7. Ehime Pref., Ishizuchi Range, Omogo, 730 m, 16142, 56+1. — 8. Do., Ishizuchi Range, Mt. Kamegamori, Himinisengoku, 1690-1730 m, 16299~300, 16314, 16337, 56; 16314, ca. 56; 16333, 16339, 56+1. — 9. Do., Akaishi Range, Tonaru to Dozangoe, 650-1100 m, 17088, 17114, 17116, 42+1; 17113, 43; 17112, 17117, 56; 17115, ca. 56; 17111, 57; 17089, 56+2; Mt. Nishiakaishiyama, 1380-1500 m, 17093, 42+1; 17102, 17104, 43; 17090, 56.

Chugoku District. 10. Shimane Pref., Mt. Sanbe, Otokosanbe, Inumodoshi, 1050 m, 19088~9, ca. 42; 19090, 42+1. — 11. Tottori Pref., Mt. Daisen, Daisenji to summit, 950-1250 m, 19100, ca. 42; 19102, 43; 19091, 19094~5, 19098~9, 43; 19093, ca. 56; 19101, 57; summit area, 1600-1710 m, 19107, 42; 19106, 19108~9, 43; 19110, 19114, 56; 19112~3, 57; 19111, ca. 57.

Kinki District. 12. Hyogo Pref., Mt. Hyonoson, Goshikiiwa, 1400 m, 19277, 42; 19225~6, 43; Goshikiiwa to Hyonosengoe, 1350 m, 19230, 19232, 43. — 13. Shiga Pref., Mts. Hirasano, In-Valley, 220-230 m, 19240, 19246, ca. 42; 19238, 19249~50, 43; Yagumogahara, 960 m, 19242, 19244, 42; 19245, 44. — 14. Do., Mt. Ibuki, 1250 m, 19253, ca. 56; 19252, 57. — 15. Nara Pref., Mt. Sanjogatake, Rengetsuji to summit, 1520 m, 16387, 42; 1670 m, 16391, 42. — 16. Do., Mt. Inamuragatake, Dorokawa to Sanjotsuji, 960 m, 16341, 42+1; 1500-1530 m, 16342, 16344, 49; 16343, ca. 49; Sanjotsuji to summit, 1560-1620 m, 16346, ca. 42; 16364, 42+1; 18102, ca. 44. — 17. Do., Mt. Misen, flat summit area, 1880-1890 m, 18200, 56; 18195, 18198, 57; summit of Hakkenzan, 1910 m, 18220, 56. — 18. Do., Mt. Ōdaigaharayama, Daijagura, 1570 m, 16405, 42+1; 16406, 43; Shiokaradani, 1380 m, 16417, ca. 42. — 19. Mie Pref., Mt. Gozaisho, near Yunoyama Spa, 360 m, 19289, 42; 19287, 42+1; Yunoyama Spa to summit, 850-950 m, 19327~8, 42; 19324, 43; summit area, 1150-1200 m, 19292, ca. 42; 19302, 43; 19311, ca. 43; 19296, 54.

Chubu District. 20. Ishikawa Pref., Mt. Hakusan, Bettodani to Jinnosuke Hut, 1380-1500 m, 16527, 42; 16528, 43; 16529, ca. 57; 1820 m, 16532~3, 57; Murodo to Minamiryugababa, 2100-2300 m, 16561, 16626, 56. — 21. Gifu Pref., Yoshiki-gun, Kamitakaramura, near Shin-Hotaka Spa, 1250 m, 20860, 56+1; Wasabidaira to Kagamidaira, 1700 m, 20858, 42+1. — 22. Nagano Pref., Hida Range, Mt. Chogatake, 2400 m, 17536, 56+1. — 23. Do., Hida Range, Mt. Jōnen, Susado to Jōnen Hut, 1320 m, 17500~1, 42+1; 1500 m, 17502, 43; 1700 m, 17506, 44; 17505, 57. — 24. Do., Ōmachi, Takase Dam to Yumata, 1380 m, 20626~7, 43; Mt. Yumata-dake, 2280 m, 20642, 57. — 25. Do., Shirabidaira (foot of Mt. Kiso-Komagatake), 1700-1750 m, 20487, 43; 20481, 57. — 26. Do., Akaishi Range, Mt. Senjōgatake, Kitazawatoge to summit, 2000-2520 m, 17462, 56+1; 17457, 17463, 17498, 57. — 27. Do., Akaishi Range, Sanpuku Pass, Shiokawa course, 2200 m, 15415, 56+1. — 28. Do., Akaishi Range, Mt. Arakawadake, Takayamaura to summit, 2580 m, 13507, 56. — 29. Shizuoka Pref., Misakubo, Sannokyo, 380-400 m, 20074, 56; 20076, 20079, 57. — 30. Do., Sumatakyo, 550 m, 19056, 19059~61, 19063~77, 19079~80, 28. — 31. Do., Haibara-gun, Okuizumi, 500 m, 19055, 19081~2, 19085~7, 28; 19083, 56. — 32. Do., Abe-gun, Ikawa, Ikawa Station to Ikawa-honson, 700-750 m, 19017, 19022, 19045, 19048, 19050, 28; 19023, 19049, 42; 19021, 19024, 43; 19018, 19051, 56; 19016, 19053, ca. 56; near Ikawa Bridge, 700 m, 19025, 19027~8, 19030~2, 19034, 28; 19026, 28+1; Ikawa Bridge to Ikawa-honson, 700-750 m, 19035~6, 19038~43, 28; 19037, ca. 28; 19044, 56. — 33. Do., Shizuoka City, Yokozawa, 300 m, 13658, 56. — 34. Do., Umegashima, Umegashima Spa to Abetoge, 920-1300 m, 17158~9, 17161, 17165~72, 17175~9, 17182~91, 28; Umegashima Spa to Mikōchi, 800-850 m, 17194~8, 28; Mikōchi to Ōtaki, 800-950 m, 17199~202, 17204~5, 17207, 28. — 35. Yamanashi Pref., Mt. Fuji, Komitake, 2350 m, 20133, 28. — 36. Do., Mt. Mitsutoge, Shimokurechi to summit, 1000-1680 m, 15368, 15371, 15375, 15379, 15382, 15384~9, 15394, 28; 15373, 15383, ca. 28; 15378, ca. 42; 15366, 15380, 43; 1700 m,

15406, 42: summit to Hahanoshirataki, 1360 m, 15409, 28. — 37. Do., Mt. Kentotu, Tokuwa to Kokushigahara, 1150~1450 m, 17126~7, 17130, 42; 17125, 42+1; 17124, 17137, 43; 17122, ca. 44; 17131, 17135, 56; 17123, 17132, ca. 56: Kokushigahara to Tsukimiwa, 1550-1750 m, 17145, 42; 17146~7, 42+1; 17148~50, 17152, 56+1.

Kanto District. 38. Kanagawa Pref., Tanzawa, Mt. Ooyama, 850-1250 m, 20082, 20085~6, 20089~92, 28: Yabitsu Pass, 760 m, 20093~5, 28. — 39. Saitama Pref., Okumusashi, Mt. Izugatake, 700-850 m, 19010, 42; 19011, 42+1; 19012, 50; 19014, 56. — 40. Ibaraki Pref., Mt. Tsukuba, summit area, 830-876 m, M18431, M18441, M18447, M18449, 42; M18445~6, 43. — 41. Tochigi Pref., Mt. Kôshinzan, 1000 m, M17921, 43.

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Received February 6, 1984