

Variation of Chromosome Pairings in Various Clones of Garlic, *Allium sativum* L.

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Introduction

Garlic is one of the ancient condiment vegetables. It is only asexually propagated by the planting of the cloves or the bulbils. It has developed into a vegetable containing many local clones through a long cultivating history, though its improvement has been limited to selection or mutation. The karyotypic analyses of various clones have been tried by many workers, but the meiotic behaviors of the chromosomes in garlic have been investigated by only a few workers. This may result from that in some clones no seed stalks develop, or that few flowers are formed amongst the bulbils in the spathes. Garlic is one of the completely sterile plants, and the pollens degenerate at the infantile stage of microspores. This is the reason why the chromosome pairing at meiosis in garlic has been carefully observed. Several workers reported eight bivalents of 16 chromosomes in garlic^{5,7-11,13}). A few workers reported multivalent chromosomes or desynapsis^{2,5,15,16}), and the author reported a clone with an octovalent and four bivalents¹). It was interesting to study chromosome pairings at meiosis in various clones of garlic for the purpose of clarifying the variation of the chromosome structure. This investigation was made to reveal how garlic, as a vegetatively propagated plant, has been varied in relation to the chromosome pairing at meiosis, or the chromosome structure.

Materials and Methods

The materials used here were 43 clones shown in Table 1. No.5 and 40 clones were offered by Mr. Y. Tashiro, Saga Univ., and Assistant Prof. T. Johjima, Kagoshima Univ., respectively. No.15, 17 and 31 clones were offered by Tokushima Agricultural Experiment Station. The rest of the clones were offered by Saga-ken Hatachi Einō Shidōsho (Bureau of Upland Field Crops, Saga Prefecture). All of these clones were grown for five or six years at Kagoshima University, Kagoshima. 'Shanghai-wase' clone was investigated before¹), but it was a clone collected in the population at Karatsu, Saga. 'Shanghai-wase' clone from Tokushima was investigated here.

The bulbs of all the clones were planted at Kagoshima University in September 1977, and in the next May their flower buds were picked and fixed in Farmer's fluid after having examined the stage of meiosis in the respective clone. The anthers were smeared in iron-acetocarmine solution, and the meiotic behavior of the chromosomes in pollen mother cells was examined at diplotene, diakinesis or metaphase-I, respectively.

Table 1. Chromosome pairings at meiosis

Clone	Number of pollen mother cells						Other configurations ^{3*}	Total
	$1_x + 3_{II}$ $r^{1*} c^{2*}$	$1_{VIII} + 4_{II}$ $r c$	$1_{VI} + 5_{II}$ $r c$					
1. Amami-2		4	3	2	4			13
2. Chiba-A				13	1			14
3. Chiba-B				5	4			9
4. Chili				22	5			27
5. Colombia		1		5				6
6. Hamamatsu				8	8	1f		17
7. Hokkaidō		1	5		1	1e		8
8. Howaito- Roppen (Ishikawa)		2						2
9. Howaito-Roppen (Niigata-Kubiki)		5	5					10
10. Howaito-Roppen (Tottori)		2	1					3
11. Howaito-Napori		10	14	1		1c	5g	31
12. Ibaraki				13	10			23
13. Iki-No. 1				18	7			25
14. Iki-No. 3		7	13					20
15. Iki-wase		6	3			3b	1g 2h	15
16. Iki-shu	1	7	5		1	3b	1e 2h	20
17. Kagawa-howaito- Roppen (Tokushima)		6	3					9
18. Kagoshima-A				5	3			8
19. Kagoshima-zairai				14	5			19
20. Kankō				10	5			15
21. Kōchi				12	1			13
22. Kōchi-daikyū		11	11			1e		23
23. Kōchi-shōkyū				15	5			20
24. Kōchi-zairai				40	7	1c	1i	49
25. Kōkotsu	5 10		3			1a	1d	20
26. Niigata				5	4	1f		10
27. Okute-B				16	15	2f	2j 1k	36
28. Roppen-shu		7	4			1b	1h	13
29. Saga-Ariura				29	3	1i		33
30. Saga-zairai		3	4			1b	1e 1g	10
31. Shanhai-wase		39	31					70
32. Shimane-Tsunozu				12	4			16
33. Shizuoka-wase				9	2			11
34. Shizuoka-zairai				8	1			9
35. Taichū-Nankotsu		8	9		1			18
36. Taiwan		8	8					16
37. Taiwan-ooninniku-B		14	6		3			23
38. Taiwan-shōkyū-pinku				4	4			8
39. Tochigi-Roppen				7	3	1f		11
40. Tokushima-zairai				9	6			15
41. Toroku-kuroba-Kōkotsu		10	8					18
42. U.S.A.		8	9		6	1g		24
43. Wase-ninniku		2	3					5
Total								766

1* ring multivalents

2* chain multivalents

3* a:1_{VII} + 1_{III} + 3_{II}, b:1_{VII} + 4_{II} + 1_I, c:1_{VI} + 1_{IV} + 3_{II}, d:2_V + 3_{II}, e:1_V + 1_{III} + 4_{II}, f:1_V + 5_{II} + 1_I, g:2_{IV} + 4_{II}, h:1_{IV} + 1_{III} + 4_{II} + 1_I, i:1_{IV} + 6_{II}, j:1_{IV} + 5_{II} + 2_I, k:2_{III} + 5_{II}.

Results

Chromosome pairings of all the examined clones are shown in Table 1, and their typical configurations are shown in Figs. 1–36. All of the clones showed multivalent chromosomes in their pollen mother cells, and there was no detection of pollen mother cells involving eight bivalent chromosomes. The multivalents were observed at diplotene through metaphase-I, and they were noted to be made of the chromosomes tightly held together, though some multivalents were sticky. Both of the ring multivalents and the chain multivalents were observed in most of the clones, as shown in Table 1. Basing on those mentioned above, the multivalents observed here were assumed not to be pseudomultivalents¹⁴⁾.

All or most of the pollen mother cells in a clone showed a chromosome configuration, which might possibly be represented by one schema, as $(1_{VI} + 5_{II})$ in No.2 clone, except those in No.1 clone. The chromosome configuration $(1_X + 3_{II})$ was observed in most of PMCs of No.25 clone. The chromosome configuration $(1_{VIII} + 4_{II})$ was observed in all or most of PMCs in nineteen clones, Nos.7–11, 14–17, 22, 28, 30, 35–37, 41–43. The chromosome configuration $(1_{VI} + 5_{II})$ was observed in all or most of PMCs in twenty-two clones, Nos.2–6, 12, 13, 18–21, 23, 24, 26, 27, 29, 32–34, 38–40. About half of the pollen mother cells in No.1 clone showed the chromosome configuration $(1_{VIII} + 4_{II})$, the rest of them showing the chromosome configuration $(1_{VI} + 5_{II})$. Consequently all the examined clones were fundamentally classified, according to the chromosome configuration represented by the schema $(1_X + 3_{II})$, $(1_{VIII} + 4_{II})$ or $(1_{VI} + 5_{II})$.

The examined clones are also classified into two large groups according to their sources, namely, the local group in Japan and the group introduced into Japan.

First, the local clones are listed in Table 2. Some of the local clones may be subdivided into small groups by the locality. No.2 and 3 clones rightly belong to 'Chiba-zairai', one of the leading varieties in Japan. 'Chiba-zairai' clone has been cultivated originally in Chiba Prefecture. Both of No.2 and 3 clones showed the same chromosome configuration, $(1_{VI} + 5_{II})$ (Figs. 2, 3). No.18 and 19 clones might be originated from the same population, because they came from the same area, Kagoshima. Both of them showed $(1_{VI} + 5_{II})$ (Figs. 15, 16). No.1 'Amami-2' clone also came from the same prefecture, but it may be put into another group, since its appearance differs much from those of No.18 and 19 clones. Amami island is far from the main land, belonging to the subtropical zone. No.1 clone did not have a main chromosome configuration, such as those of other clones, so that it was not shown in Table 2. Further investigation may be necessary for No.1, because in this investigation enough PMCs at the right stage of meiosis could not be observed on account of the limited number of the flower buds. No.21–24 clones rightly belong to 'Kōchi-zairai' clone, one of the leading varieties in Japan. 'Kōchi-zairai' clone has been cultivated in Kōchi Prefecture. No.21, 23 and 24 clones showed the same chromosome configuration $(1_{VI} + 5_{II})$ (Fig.19), but No.22 'Kōchi-daikyū' showed $(1_{VIII} + 4_{II})$ (Fig.18). 'Daikyū' means 'a big bulb'. 'Kōchi-

Table 2. Sources and chromosome pairings of the local clones in Japan

Chromosome configuration	Clone No.				
	Chiba	Kagoshima	Kōchi	Shizuoka	Other areas
$1_X + 3_{II}$					
$1_{VIII} + 4_{II}$			22		7,43
$1_{VI} + 5_{II}$	2,3	18,19	21,23,24	33,34	6,12,26,27,32,40

daikyū' clone must have been selected, as a strain characterized by its bigness, from 'Kōchi-zairai' clone. No.33 and 34 clones rightly belong to 'Shizuoka-zairai' clone, one of the leading varieties in Japan. The chromosome configuration of No.33 and 34 clones was ($1_{VI} + 5_{II}$) (Fig.28). No.6, 7, 12, 26, 32 and 40 clones must be the local varieties established in the respective areas. No.6 clone rightly belongs to 'Enshū-gokuwase' clone, one of the leading varieties in Japan. No.7 clone rightly belongs to 'Furano' clone, one of the leading varieties in the cool region of Japan. The chromosome configuration of those five clones except No.7 was ($1_{VI} + 5_{II}$) (Figs. 6, 7, 10, 21, 27, 33).

In short, most of the local clones similarly showed the chromosome configuration ($1_{VI} + 5_{II}$). No.27 and 43 clones were supposed to be belonging to the local clones in Japan, but it was not clear where they came from.

Next, the clones which were probably introduced into Japan are listed in Table 3.

Table 3. Sources and chromosome pairings of the introduced clones

Chromosome configuration	Clone No.					
	China	(Iki)	Korea (Roppen)	(Saga)	Taiwan	Other countries
$1_X + 3_{II}$	25					
$1_{VIII} + 4_{II}$	31,41	14,15,16	8,9,10,28	17,30	35,36,37	11,42
$1_{VI} + 5_{II}$	20	13	39	29	38	4,5

No.20, 25, 31 and 41 clones were introduced from China. No.25 'Kōkotsu' is a clone well-known in China¹²⁾, and No.41 must be derived from the population of 'Kōkotsu' clone. In China, however, there is a large group of the clones named 'Kōkotsu-shu', so that nobody can reasonably conclude that all the clones of the group have the same origin. 'Shanghai-wase' (No.31) is the Japanese name of 'Katei' clone in China. The chromosome configurations of the clones from China showed the widest variability among those of the subdivided groups examined (Figs. 17, 20, 26, 34). The chromosome configuration of 'Shanghai-wase' (Tokushima) clone was ($1_{VIII} + 4_{II}$), which was similar to that of the clone from Karatsu¹⁾. No.13-16 clones rightly belong to 'Iki-wase' (or 'Ishū-wase') clone, one of the leading varieties in Japan, introduced from Korea¹²⁾. The clones of 'Iki-wase' group except No.13 showed the chromosome configuration ($1_{VIII} + 4_{II}$) (Figs. 11-13). 'Roppen-shu' clone is also one of the leading varieties in Japan. It was estimated that the clone was, originally, introduced from Korea¹²⁾, but it is not clear whether all the strains of 'Roppen' were derived from the same origin or not, because there are so many strains of 'Roppen' throughout Japan. In this investigation, all of the 'Roppen' strains were put into one group for convenience. No.8-10 and 28 clones showed ($1_{VIII} + 4_{II}$), while No.39 clone showed ($1_{VI} + 5_{II}$) (Figs. 8, 23, 32). No.17, 29 and 30 clones were estimated to be belonging to one group. No.17 'Kagawa-howaito-Roppen' clone was derived from 'Kagawa-Roppen' clone. 'Kagawa-Roppen' was derived from 'Saga-ooninniku' clone, which must be derived from 'Saga-zairai' clone, one of the leading varieties in Japan, introduced from Korea¹²⁾. No.29 clone was cultivated at Ariura, Saga Prefecture. It maybe belongs to 'Saga-zairai' clone. No.17 and 30 clones showed ($1_{VIII} + 4_{II}$), while No.29 showed ($1_{VI} + 5_{II}$) (Figs.14, 24, 25). No.35-37 clones were introduced from Taiwan. No.35 'Taichū-Nankotsu' clone might originally be introduced from China to Taiwan, because 'Nankotsu-shu' is a clone well-known in China¹²⁾. The chromosome configuration of No.35-37 clones showed ($1_{VIII} + 4_{II}$), while No.38

'Taiwan-shōkyū-pinku' showed ($1_{VI} + 5_{II}$) (Figs.30, 31). 'Shōkyū' and 'pinku' mean 'a small bulb' and 'pink', respectively. No.4, 5 and 42 clones were introduced from the respective countries, as shown in Table 1. No.11 'Howaito-Napori' clone must be introduced from Italy. 'Howaito' and 'Napori' mean 'white' and 'Naples', respectively. The chromosome configuration of No.11 and 42 clones showed ($1_{VIII} + 4_{II}$), and No.4 and 5 clones showed ($1_{VI} + 5_{II}$) (Figs.4, 5, 9, 35).

After all, most of the introduced clones showed the chromosome configuration ($1_{VIII} + 4_{II}$).

Discussion

The chromosome pairings at meiosis of several clones in garlic, *A. sativum* L. were reported as eight bivalents by some workers, and as multivalents by a few workers. It was expected, before this investigation, that some of 43 clones might have eight bivalents. However, all of 43 clones showed more than one multivalent in all the pollen mother cells. None of the 766 examined pollen mother cells showed eight bivalents at meiosis.

Thirty-nine of 43 clones examined here came from East Asia, namely, China, Japan, Korea and Taiwan. In ancient times garlic must have been introduced from Central or West Asia to China⁶⁾, and then to Taiwan, to Korea, or to Japan. Hence, all of the local clones in Japan are supposed to have been introduced in any case. In this investigation, the clones from China showed the widest variation in the chromosome pairing. And moreover, garlic has a great number of local clones in China¹²⁾. Garlic may have been varied much in China, both karyologically and morphologically. Therefore, it seems very interesting to investigate as many local clones as possible in China.

The chromosome configurations of the examined clones were almost similar to each other within a small subdivided group, such as 'Chiba' or 'Saga'. Most of the local clones in Japan showed hexavalents (Table 2). Most of the clones introduced from China, Korea and Taiwan showed octovalents (Table 3), which were higher multivalents than hexavalents of the local clones in Japan. Octovalents are usually formed from hexavalents. The clones with hexavalents may have an origin different from the clones with octovalents, or both of them may have a common ancestor, such as a clone with hexavalents or quadrivalents.

The clone groups of 'Chiba', 'Iki', 'Kōchi', 'Saga' and 'Shizuoka' include 15 clones of the examined clones, and they are the leading varieties in the warm regions of Japan. Kagoshima is situated in the warm region. In the warm region, or in the clones from the warm region, the chromosome mutation in garlic may be tending to occur—reciprocal translocations, for example. Besides those groups mentioned above, there were some clones from the warm regions among the examined clones (Nos.1, 4, 12, 18-20, 31, 35-38, 40, 43). On the other hand, there were a few clones from the cool region (Nos.6, 7). 'Roppen' group is sometimes regarded as a clone group in the cool region, though it has been cultivated throughout Japan. Therefore, more clones from the cool region should be investigated cytologically.

When did the structural chromosome changes observed here occur? They might have occurred independently in the somatic cells of the genetically isolated clones. If garlic had been fertile, some of them might have come from the structural variation having existed in the original sexual population.

Konvicka and Levan⁹⁾ examined a clone with a quadrivalent, and they found it to

correspond to *Allium longicuspis* Regel by a preliminary taxonomic determination. It may be possible for some species to mix with garlic. The clone with a quadrivalent, called LH clone, was originally introduced from the Moscow botanic garden into Lund, Sweden. Konvicka and Levan⁹⁾ also observed eight bivalents in a clone from Olomouc, Czechoslovakia. *A. longicuspis* Regel is the wild race of *A. sativum* L., according to Vvedensky¹⁸⁾. There may be the need to carry out the detailed cytological investigation of *A. longicuspis* Regel. The origin of the clones with eight bivalents may differ from that of those with multivalents.

Today, more than 600 species are recognized in the genus *Allium*. A few taxonomists tried to set the family *Alliaceae*, instead of the genus *Allium*¹⁹⁾. The genus *Allium* might be a large genus giving addition to the number of species, and the species of the genus *Allium* may vary frequently. Garlic is an extremely variable species⁴⁾. There are three or four botanical varieties in *A. sativum* L. Helm³⁾ showed three varieties, *var. sativum*, *var. ophioscordon* (Link) Döll and *var. pekinense* (Prok.) Maek. According to Kitamura⁶⁾, garlic cultivated in China is *A. sativum var. pekinense* (Prok.) Maekawa, and garlic cultivated in Japan is *var. japonicum* Kitam. He also stated that 'Kökotsu' clone in Taiwan was similar to *A. sativum* in Europe⁶⁾.

Karyological evolution in the genus *Allium* was studied frequently, before. On the structural chromosome changes in the genus *Allium*, Traub¹⁷⁾ stated, "The main value of the structural chromosome changes lies in the production of rapid evolutionary changes. The chief drawback is that it may lead to sterility. In those cases where it has a high survival value, species evolution is rapid and marked." The wide chromosomal variation in garlic may be the product of "rapid evolutionary changes". Chromosomal changes are supposed to have occurred so frequently in garlic, and the variants which result from the chromosomal changes have a tendency to be well preserved by vegetative propagation. Some of the rapid evolutionary changes may have resulted from the accumulation of chromosome mutation. Chromosomal changes in garlic may tend to be accumulated more than those in other vegetatively propagated plants. Garlic is a crop in which any variant tends to be selected. The edible part of garlic, bulb, is used as the vegetatively propagated part, though young leaves are used as food in some area. And moreover, a garlic bulb can be divided into several cloves, sometimes into a lot of cloves. As garlic is a kind of condiment vegetable, the cloves are not used in large quantities at a time. Therefore, some cloves of a variant bulb might be left to be used as "seeds". Garlic is not so difficult to be carried, to be stored or to be grown. During the long cultivating history, it was dispersed gradually and developed into many local clones, which must have been resulted in the formation of wide karyological variations. High adaptability of garlic may represent its high variability of the chromosome structure. It would be interesting to investigate the correlationship between the chromosome variants and the properties of the clones.

Summary

Chromosome pairings at meiosis were examined in 43 clones of garlic, *Allium sativum* L. Most of the examined clones originally came from China, Japan, Korea and Taiwan. All the clones regularly showed multivalents. Eight bivalents of 16 chromosomes were not observed in any of the 766 pollen mother cells. The chromosome configuration ($1_{VI} + 5_{II}$) was observed in all or most of the pollen mother cells of 22 clones. The chromosome con-

figuration ($1_{VIII} + 4_{II}$) was observed in all or most of the pollen mother cells of 19 clones. Fifteen clones of the former were the local clones in Japan, while sixteen clones of the latter were those introduced into Japan in recent times. A clone from China showed the chromosome configuration ($1_X + 3_{II}$). One from Amami, a southern island of Japan, showed ($1_{VI} + 5_{II}$) and ($1_{VIII} + 4_{II}$) in almost the same number of PMCs, respectively. A subdivided clone group, which must have been originated in the same population, showed almost the same chromosome configuration.

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Explanation of figures

- Figs. 1–36. Chromosome pairings of the clones at meiosis.
- Fig. 1. No. 1 'Amami-2' clone, ($1_{VI} + 5_{II}$), \times ca.950.
- Fig. 2. No. 2 'Chiba-A' clone, ($1_{VI} + 5_{II}$), \times ca.950.
- Fig. 3. No. 3 'Chiba-B' clone, ($1_{VI} + 5_{II}$), \times ca.400.
- Fig. 4. No. 4 'Chili' clone, ($1_{VI} + 5_{II}$), \times ca.750.
- Fig. 5. No. 5 'Colombia' clone, ($1_{VI} + 5_{II}$), \times ca.950.
- Fig. 6. No. 6 'Hamamatsu' clone, ($1_{VI} + 5_{II}$), \times ca.750.
- Fig. 7. No. 7 'Hokkaidō' clone, ($1_{VIII} + 4_{II}$), \times ca.750.
- Fig. 8. No. 9 'Howaito-Roppen' (Niigata-Kubiki) clone, ($1_{VIII} + 4_{II}$), \times ca.950.
- Fig. 9. No. 11 'Howaito-Napori' clone, ($1_{VIII} + 4_{II}$), \times ca.950.
- Fig. 10. No. 12 'Ibaraki' clone, ($1_{VI} + 5_{II}$), \times ca.950.
- Fig. 11. No. 13 'Iki-No. 1' clone, ($1_{VI} + 5_{II}$), \times ca.750.
- Fig. 12. No. 14 'Iki-No. 3' clone, ($1_{VIII} + 4_{II}$), \times ca.950.
- Fig. 13. No. 15 'Iki-wase' (Tokushima) clone, ($1_{VIII} + 4_{II}$), \times ca.750.
- Fig. 14. No. 17 'Kagawa-howaito-Roppen' (Tokushima) clone, ($1_{VIII} + 4_{II}$), \times ca.750.
- Fig. 15. No. 18 'Kagoshima-A' clone, ($1_{VI} + 5_{II}$), \times ca.950.
- Fig. 16. No. 19 'Kagoshima-zairai' clone, ($1_{VI} + 5_{II}$), \times ca.950.
- Fig. 17. No. 20 'Kankō' clone, ($1_{VI} + 5_{II}$), \times ca.950.
- Fig. 18. No. 22 'Kōchi-daikyū' clone, ($1_{VIII} + 4_{II}$), \times ca.750.
- Fig. 19. No. 24 'Kōchi-zairai' clone, ($1_{VI} + 5_{II}$), \times ca.750.
- Fig. 20. No. 25 'Kōkotsu' clone, ($1_X + 3_{II}$), \times ca.950.
- Fig. 21. No. 26 'Niigata' clone, ($1_{VI} + 5_{II}$), \times ca.650.
- Fig. 22. No. 27 'Okute-B' clone, ($1_{VI} + 5_{II}$), \times ca.950.
- Fig. 23. No. 28 'Roppen-shu' clone, ($1_{VIII} + 4_{II}$), \times ca.750.
- Fig. 24. No. 29 'Saga-Ariura' clone, ($1_{VI} + 5_{II}$), \times ca.950.
- Fig. 25. No. 30 'Saga-zairai' clone, ($1_{VIII} + 4_{II}$), \times ca.950.
- Fig. 26. No. 31 'Shanghai-wase' (Tokushima) clone, ($1_{VIII} + 4_{II}$), \times ca.950.
- Fig. 27. No. 32 'Shimane-Tsunozu' clone, ($1_{VI} + 5_{II}$), \times ca.950.
- Fig. 28. No. 34 'Shizuoka-zairai' clone, ($1_{VI} + 5_{II}$), \times ca.950.
- Fig. 29. No. 35 'Taichū-Nankotsu' clone, ($1_{VIII} + 4_{II}$), \times ca.950.
- Fig. 30. No. 36 'Taiwan' clone, ($1_{VIII} + 4_{II}$), \times ca.950.
- Fig. 31. No. 38 'Taiwan-shōkyū-pinku' clone, ($1_{VI} + 5_{II}$), \times ca.950.
- Fig. 32. No. 39 'Tochigi-Roppen' clone, ($1_{VI} + 5_{II}$), \times ca.950.
- Fig. 33. No. 40 'Tokushima-zairai' clone, ($1_{VI} + 5_{II}$), \times ca.750.
- Fig. 34. No. 41 'Toroku-kuroba-Kōkotsu' clone, ($1_{VIII} + 4_{II}$), \times ca.950.
- Fig. 35. No. 42 'U.S.A.' clone, ($1_{VIII} + 4_{II}$), \times ca.950.
- Fig. 36. No. 43 'Wase-ninniku' clone, ($1_{VIII} + 4_{II}$), \times ca.750.



