CYTOGENETICAL STUDIES ON CAMELLIA SPECIES

I. The Meiosis and Gametogenesis of *Camellia wabiske* Compared with *C. japonica* and *C. sinensis*

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Synopsis. In *Camellia wabiske* the normality of meiosis and formation of anthers and embryo sacs were different according to the variety. In both SUKIYA-WABISUKE and USU-WABISUKE there were more or less abnormal meiosis, while in KOTYO-SIRO-WABISUKE no anthers and embryo sacs were formed. From these results it was considered that there was a little homology among the chromosomes in *C. wabiske*. At megasporogenesis only dyads were formed in embryo sac mother cells. In *C. wabiske*, abnormal formation of anthers and embryo sacs occurred by the abnormal growth at a very young stage, and this abnormality was related to the time interval between microsporogenesis and megasporogenesis.

Introduction

For breeding of cold resistant varieties of the tea plant, a number of attempts of hybridization between *C. sinensis* and other *Camellia* species have been made for many years. However, some hybrids between *C. sinensis* and *C. sasanqua* were successfully made recently, while the hybridization between *C. sinensis* and *C. japonica* was not yet successful, although both the parents have the same chromosome number.

Some botanists consider *C. wabiske* as a variety of *C. reticulata*, while the others consider it as a hybrid between *C. sinensis* and *C. japonica* (KITAMURA, 1965). If the latter be true, then there will be a lot of possibility of acquiring hybrids by crossing *C. sinensis* with *C. japonica*. In the light of this con-

sideration, the authors have been carrying out several experiments by crossing *C. sinensis* with *C. japonica*. The present studies are reported only on the meiosis and gametogenesis as well as the formation of anthers and embryo sacs in *C. wabiske* and is compared with *C. sinensis* and *C. japonica*.

Materials and Methods

Table 1 shows the materials used in the present studies. They were collected from the field of the Faculty of Agriculture, Nagoya University, Nagoya.

Cytological method: For the observation of meiosis in PMCs the fresh young flower buds collected were immediately put in 60°C 1N-HCl for 5 min and washed with water followed by smearing under the cover-glass with 1% aceto-orcin without using any fixing re-

Table 1. Varieties used as the experimental materials

Species	Variety	Chromosome number
<i>Camellia sinensis</i> L.	YABUKITA	2n=30
<i>C. japonica</i> Linnaeus var. <i>spontanea</i> Makino	YABUTUBAKI	2n=30
<i>C. wabiske</i> Kitamura	KOTYO-SIRO-WABISUKE	2n=30
	AKA-WABISUKE	2n=30
	SIRO-WABISUKE	2n=30
	USU-WABISUKE	2n=30
	SUKIYA-WABISUKE	2n=30

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agent.

The pollen-fertility was examined by the smear method with aceto-carmin solution. By the degree of staining reaction to aceto-carmin, the pollen-fertility was determined. The pollen grains stained deep were recognized as fertile ones.

Histological method: For observing the development of anther and ovule tissues, the young flower-buds in their proper stages of growth were fixed with FAA (Formalin-Acetic

acid-Alcohol) or Craf fluid. After dehydration the materials were embedded in paraffin and cut in 10 or 12 μ thickness. Though some sections were stained with Delafield's hematoxylin, most of the sections were hydrolyzed in 60°C 1N-HCl for 10 min and were stained with Feulgen's fluid.

Results

Cytological observation

In *Camellia sinensis* and *C. japonica*, meiosis

Fig. 1. Meiosis in PMCs in *C. sinensis*, *C. japonica* and *C. wabisuke*. A. Metaphase I in *C. japonica*. 15 bivalent chromosomes are observed. $\times 1000$. B. Diakinesis in *C. wabisuke* (USU-WABISUKE). $\times 1300$. C. Metaphase II in USU-WABISUKE. Small stray chromosomes are seen. $\times 700$. D. Tetrads and dyads in USU-WABISUKE. Dyads with micro-nuclei are observed. $\times 300$. E. Tetrads, dyads and those with micro-nuclei in SUKIYA-WABISUKE. $\times 100$. F. Anaphase I in SUKIYA-WABISUKE. Lagged chromosomes are observed. $\times 1000$.

Table 2. Frequency of univalents appeared at anaphase I and metaphase II in *C. wabiske*

Variety	The number of univalents					Total number of PMCs	% of univalents () The mean % of univalents
	0	1	2	3	4		
SUKIYA-WABISUKE	33	5	2	1	2	43	23.3
	43	4	2			49	21.2
							(17.8)
USU-WABISUKE	57		1	1		59	3.4
	153	10				163	6.3
	72	6	1			79	8.9
	46	7				53	13.2
							(7.9)

Table 3. Various types of sporads in pollen tetrad stage of *C. wabiske*

Variety	Dyads	Tetrads	Sporads with micronuclei
SUKIYA-WABISUKE	70.4%	28.2%	18.2%
USU-WABISUKE	8.1	89.0	6.7

Table 4. The pollen fertility

Species	Pollen fertility
<i>C. sinensis</i>	85.4%
<i>C. japonica</i>	85.7
SIRO-WABISUKE	84.5
AKA-WABISUKE	77.2
USU-WABISUKE	20.8
SUKIYA-WABISUKE	2.8

Table 5. The percentage of normal anthers

Species	The part of the anther		
	Upper	Middle	Lower
<i>C. japonica</i>	100%	100%	100%
SIRO-WABISUKE	100	100	100
AKA-WABISUKE	100	100	100
USU-WABISUKE	68.7	78.9	67.9
SUKIYA-WABISUKE	8.3	31.7	38.9
KOTYO-SIRO-WABISUKE	0	0	0

Transverse sections of anthers were made and were divided into three parts: upper, middle and lower. Each part of the anther was separately observed.

was normal at the metaphase I and 15 bivalent chromosomes were observed (Fig. 1). But in *C. wabiske*, the behavior of chromosomes at meiosis varied according to variety. The varieties of *C. wabiske*, AKA-WABISUKE and SIRO-WABISUKE showed almost the same behavior of chromosomes at meiosis as in *C. sinensis* and *C. japonica*, while in SUKIYA-WABISUKE and USU-WABISUKE, many univalents were observed at anaphase I and metaphase II.

The frequency of the univalents appeared at the anaphase I and metaphase II was more in SUKIYA-WABISUKE than in USU-WABISUKE, and in the former some chromosome bridges were also observed (Table 2). In KOTYO-SIRO-WABISUKE pollen grains could not be observed due to the failure of the development of anthers (Table 5).

The type of the sporads in the pollen tetrad stage was generally tetrad in *C. sinensis*, *C. japonica*, AKA-WABISUKE and SIRO-WABISUKE, but in USU-WABISUKE and SUKIYA-WABISUKE, there happened monad, dyad, triad, tetrad and the maximum novad which contained some micro-nuclei (Table 3). Further in SUKIYA-WABISUKE, the percentage of dyads to total number of PMCs was 70.4 and that of tetrads was 28.2, while in USU-WABISUKE, the percentage of dyads was 8.1 and that of tetrads was 89.0. The micro-nuclei were more numerous in SUKIYA-WABISUKE than in USU-WABISUKE (Table 3, Fig. 1).

The pollen fertility became more and more in order in *C. sinensis*, *C. japonica*, SIRO-

AKA-, USU- and SUKIYA-WABISUKE (Table 4). Moreover, in USU- and SUKIYA-WABISUKE not only giant pollen grains, but also very small pollen grains were often observed.

Histological observation

1. Morphogenesis of male and female gametophytes in *C. sinensis* and *C. japonica*.

A. Microsporogenesis. A cross section of a young anther showed a primary cell in each lobe. The cell divided periclinally into two cells, and the outer cell was a primary parietal cell, while the inner cell was an archesporial cell. As the bud grew, a primary parietal cell divided anticlinally and periclinally which

consequently gave rise to tapetal cells and a central layer. In a central layer, the cells divided periclinally which gave rise to middle layer and endothecium. Then, a middle layer formed two middle layers by periclinal division. The sporogenous cell began dividing at the tapetum, and grew into pollen mother cells. Meiosis was normal in PMCs, the pollen mother cells formed tetrads and thereafter normal pollen grains. The tapetum developed until tetrads were formed from PMCs, and cells of the tapetum consisted of cells with numerous nuclei at that time. Thereafter, the tapetum and middle layers degenerated in accordance with maturity in PMCs. As the pollens

Fig. 2. Microsporogenesis in *C. sinensis*. A. A cross section of a young anther. $\times 350$. B. Initiation of an initial cell. $\times 700$. i: Initial cell. C. An initial cell divides periclinally. $\times 700$. a: Archesporial cell. p: Parietal cell. D. Division of cells in the central layer into the endothecium and the middle layer. $\times 375$. s: Sporogenous cell. m: Middle layer. e: Endothecium. E. A cross section of an anther at the tetrad stage. $\times 100$. t: Tapetum. F. A cross section of an anther at the pollen stage. $\times 150$. p: Pollen.

matured, epidermis, endothecium, degenerated middle layers and tapetum were observed around the pollen grains (Fig. 2).

B. Megasporogenesis. The ovules were anatropous. At that time when the microsporangia were square shape in the cross sections of anthers (Fig. 2), a primary cell was observed in perpendicular position to epidermis in nucellus. This primary cell was a hypodermal archesporial cell, and functioned directly as megaspore mother cell. The megaspore mother cell formed dyad as a result of periclinal division. The outer cell degenerated as the ovule developed, the inner cell enlarged, the nucleus of the inner cell divided to form a 2-nucleate embryo sac, and the remnant of the degenerating outer cell was also observed at this stage.

The embryo sac increased in size, became vacuolate, and two-nuclei divided repeatedly into eight-nuclei. The embryo sac contained an egg cell, two synergids, two polar nuclei and three antipodal cells at the flowering time.

2. Morphogenesis of male and female gametophytes in *C. wabiske*.

A. Microsporogenesis. The gross morphol-

ogical normality of the anther in *C. wabiske* was different according to the variety. In AKA-WABISUKE and SIRO-WABISUKE, the gross morphological form was normal as in *C. sinensis* and *C. japonica*, but in USU-WABISUKE, SUKIYA-WABISUKE and KOTYO-SIRO-WABISUKE the gross morphological form was abnormal and the abnormality increased more in order in USU-WABISUKE, SUKIYA-WABISUKE and KOTYO-SIRO-WABISUKE. In USU-WABISUKE and SUKIYA-WABISUKE, some cross sections of a young anther did not show square-shape, but in this situation, four lobes were formed: there were no two-by-two lobes along the central vascular bundle of the anther, and in some anthers there were lobes only at the other side of the central vascular bundle.

And also in other anthers many lobes were formed at both sides of central vascular bundle and the number of lobes was not constant (Fig. 3). In SUKIYA-WABISUKE, such tendency decreased from the lower part of the anther to the upper part (Table 5). As the buds grew, in USU-WABISUKE and SUKIYA-WABISUKE, each lobe formed middle layers,

Fig. 3. Cross sections of anthers in *C. wabiske* (KOTYO-SIRO-WABISUKE). A. Very young stage. $\times 20$. B, C, D. Matured anthers. $\times 37.5$. v: Central vascular bundle.

Fig. 4. Cross sections of anthers in USU-WABISUKE, SUKIYA-WABISUKE and *C. japonica*. A. Matured anther in USU-WABISUKE. Abnormal lobes are observed. $\times 25$. B. Matured anther in SUKIYA-WABISUKE. Abnormal lobes are observed. $\times 25$. C. Matured anther in *C. japonica*. All the lobes are formed normally. $\times 50$.

endothecium, tapetum and pollen grains, but the developmental stage of these tissues in each lobe was not simultaneous (Fig. 3).

In KOTYO-SIRO-WABISUKE a cross section of a young anther showed variously shaped upheavals around the central vascular bundle of the anther. The number of these upheavals varied in every anther. As the buds grew further, upheavals developed in size and the cells of the central part of upheavals enlarged. Then the walls of these cells increased in thickness. In these variously shaped upheavals, endothecium, middle layers, tapetum and pollen grains did not differentiate (Fig. 3).

B. Megasporogenesis. In SUKIYA-WABISUKE and USU-WABISUKE, some ovules developed normally as that in *C. sinensis* and *C. japonica*. But in other ovules, the nucellus developed as the buds grew, and an archesporial cell did not divide distinctly. Moreover, at the maturing stage of flowers, the trace of nucellus remained in the normal position of the embryo sac (Fig. 4).

In KOTYO-SIRO-WABISUKE the gross morphological form of ovules was abnormal, and some of them were string-like whereas

Fig. 5. Gross morphological form of the anther and ovule. a. Gross morphological form of ovules in KOTYO-SIRO-WABISUKE. $\times 27$. b. Gross morphological form of an anther in *C. japonica*. $\times 6$. c, d. Gross morphological form of an anther in *C. wabiske* (KOTYO-SIRO-WABISUKE). c. $\times 10$. d. $\times 13$.

the others changed color to brown, but in some cases very solid ovules were also observed (Fig. 5). At the very young stage of developing ovules one or several cells enlarged directly under the epidermis of some nucellus, and as the ovules grew these cells enlarged more in the nucellus tissue, although 8-nuclei were not observed in such cells. Further, at the young stage, although the enlarged cells were observed in other part of nucellus tissue, the number of the enlarged cells and the position in nucellus tissue were different according to the ovules. At the maturing stage of ovules, embryo sacs were not empty, but the division of cells was abnormal or the trace of nucellus was observed instead of embryo sacs.

3. Comparison of the microsporogenesis and megasporogenesis in *Camellia sinensis*, *C. japonica* and *C. wabiske*.

USU-WABISUKE and SUKIYA-WABISUKE showed that male and female gametophytes developed abnormally, and there was less difference between the developmental

stage of male and female gametophytes than *C. sinensis*, *C. japonica* and AKA-WABISUKE in which male and female gametophytes developed normally (Table 6).

In USU-WABISUKE and SUKIYA-WABISUKE, when dyads in megaspore mother cells were formed, the parietal cell in male gametophyte divided, and at this stage of male gametophytes both nucellus and integuments initiated in female gametophyte in *C. sinensis* and *C. japonica*.

At the time when endothecium, middle layers and tapetum were completed in male gametophyte, the embryo sacs were completed in USU-WABISUKE and SUKIYA-WABISUKE, but dyads were observed in *C. sinensis* and *C. japonica*, while in *C. sinensis* and *C. japonica*, at the time of pollen formation the embryo sacs were completed (Table 6).

Discussion

At meiosis in *C. sinensis*, *C. japonica*, SIRO-WABISUKE and AKA-WABISUKE, normal

Table 6. Comparison of the microsporogenesis and megasporogenesis in *Camellia sinensis*, *C. japonica* and *C. wabiske*

Microsporogenesis	Megasporogenesis				
	<i>C. sinensis</i>	<i>C. japonica</i>	<i>C. wabiske</i>		
			AKA-WABISUKE	USU-WABISUKE	SUKIYA-WABISUKE
Archeporial cells		Ovule primordium initiates	Ovule primordium initiates	Ovule primordium develops	Integuments initiate
Parietal cells divide and sporogenous cells initiate		Integuments develops	Megaspore mother cells initiate	Dyad	Dyad
The endothecium and central layer initiate	Ovule primordium develops		Dyad		
The endothecium, middle layer and tapetum are completed	Dyad	Dyad		Eight-nuclei in embryo sac	Eight-nuclei in embryo sac
Meiosis	Two-nuclei divide in embryo sac	Four-nuclei divide in embryo sac	Eight-nuclei in embryo sac		
Pollen	Eight-nuclei in embryo sac	Eight-nuclei in embryo sac			

The first developmental tissues are observed because the developmental stage of microsporogenesis is different according to each lobe and megasporogenesis is different according to each ovule.

tetrads were observed almost in all the PMCs. But in USU-WABISUKE and SUKIYA-WABISUKE numerous micro-nuclei were observed at the tetrad stage of PMCs (Table 3). In the case of USU-WABISUKE less univalents were observed in PMCs at anaphase I and metaphase II than in SUKIYA-WABISUKE (Table 2). As regards the type of sporads are concerned, the percentage of dyads was 70.4 in SUKIYA-WABISUKE, and 8.1 in USU-WABISUKE (Table 3). The percentage of normal anthers was 26.3 in SUKIYA-WABISUKE, but 71.9 in USU-WABISUKE. And in KOTYO-SIRO-WABISUKE almost all the anthers and ovules did not develop. According to these results in *C. wabiske* the abnormal meiosis in PMCs would be related to the abnormal development in anthers. It has been reported in intergeneric hybrids of *Aegilops* $\times$ *Triticum* (KIHARA 1951), *Festuca* $\times$ *Lolium* (L.V. CROWDER 1953), *Citrus* $\times$ *Trifoliata*

(IWAMASA 1966) that the meiosis was abnormal and the developmental abnormalities of anthers and ovules were observed. Consequently it could be thought that *C. wabiske* might be a hybrid between *C. sinensis* and *C. japonica*, but in order to prove it the karyotypes of *C. sinensis*, *C. japonica* and *C. wabiske* should be investigated.

In *C. sinensis*, *C. japonica* and *C. wabiske*, a hypodermal archesporial cell functioned directly as the megaspore mother cell and the dyad was observed in nucellus. In the megasporogenesis, SIMURA and OSONE (1956), HUTINOUE and HUTINOUE (1965) observed a linear tetrad in nucellus in *C. sinensis* while KAPIL and SETHI (1963) observed a dyad only in nucellus and DAVIS (1966) reviewed the formation of dyads in *C. sinensis* at megasporogenesis. Therefore in the genus *Camellia* it was considered that dyad would be generally formed in nucellus (Fig. 6).

Fig. 6. Megasporogenesis in *C. sinensis*. A. Initiation of an archesporial cell. $\times 135$. B. Dyad. $\times 525$. C. An embryo mother cell in a nucellus. $\times 525$. D. Matured embryo sac. $\times 175$.

Fig. 7. Cross sections of the ovule and ovary in KOTYO-SIRO-WABISUKE. A. Primordia of nucellus. $\times 175$. B. Cross section of an ovary at the very young stage. $\times 60$. C, D. Ovules at the mature stage. C. $\times 1050$. D. $\times 350$. i: Inner integument. o: Outer integument.

In USU-WABISUKE, SUKIYA-WABISUKE and KOTYO-SIRO-WABISUKE the abnormality of ovules and anthers was due to the abnormal division or initiation of cells of primordia and archesporial cells in lobes and nucellus, and was due to the abnormal development at the very young stage in microsporogenesis and megasporogenesis (Fig. 7).

The difference between the stage of microsporogenesis and of megasporogenesis reveals that the interval between microsporogenesis and megasporogenesis in USU-WABISUKE and SUKIYA-WABISUKE was shorter than in AKA-WABISUKE, *C. sinensis* and *C. japonica*. In SUKIYA-WABISUKE and USU-WABISUKE the abnormal anthers, ovules and meiosis in PMCs were observed more than in AKA-WABISUKE, *C. japonica* and *C. sinensis*. Therefore, from these results it was considered that the shorter the interval between microsporogenesis and megasporogenesis was, the more abnormal anthers, ovules and meiosis in PMCs would be observed. WHYTE (1929)

observed in *Ranunculus* that in the normal hermaphrodite there was a considerable interval between reduction process in the male and female organs of the same flower, and the female flower showed these phases as entirely coincident, reduction divisions occurring almost simultaneously, and in the male plant the reduction divisions coincide as in the female flower.

Then, in order to make clear the abnormal formation of male and female gametophytes, the vascular organization should be investigated in *C. wabiske*.

Summary

For the breeding of the cold resistant variety of the tea plant, many investigators have tried hybridization between tea plants and the other *Camellia* species.

If *C. wabiske* is a hybrid between *C. sinensis* and *C. japonica* as some botanists supposed, then there will be a lot of possibility of acquiring hybrids by crossing *C. sinensis* with *C.*

japonica. Keeping this supposition into consideration the authors have been carrying out several experiments by crossing *C. sinensis* with *C. japonica*. However, the present experiments were undertaken only to observe the meiosis and gametogenesis as well as the formation of anthers and embryo sacs in *C. wabiske* and were compared with *C. sinensis* and *C. japonica*. In *C. wabiske* the normality of meiosis was different according to the variety, and in AKA-WABISUKE and SIRO-WABISUKE the meiosis as well as the gametogenesis were normal as in *C. sinensis* and *C. japonica*, while in SUKIYA-WABISUKE and USU-WABISUKE many univalents in meiosis of PMCs and many micro-nuclei at pollen tetrad stage were observed. The gametogenesis was also abnormal. The pollen sterility had a correlation with the frequency of univalents and micro-nuclei. On the other hand in KOTYO-SIRO-WABISUKE almost all the anthers and embryo sacs were not formed. From these results, it was considered that there appeared to be not much homology among chromosomes in *C. wabiske*, although according to the variety the degree of homology was different. Therefore, the karyotypes in *C. sinensis*, *C. wabiske* and *C. japonica* should be investigated later.

In microsporogenesis it was observed that a primary parietal cell divided periclinally and the outer cell gave rise to two middle layers and an endothecium, while the inner cell gave rise to tapetum. But, at the flowering time middle layers and tapetum degenerated.

At megasporogenesis in *C. sinensis* it has been reported that linear-tetrads were formed in embryo mother cells, but the present studies revealed that in *C. sinensis*, *C. japonica* and *C. wabiske* only dyads were formed.

In *C. wabiske*, abnormal formation of anthers and embryo sacs occurred by the abnormal formation of their primordia and by the abnormal division of the archesporial cells in anther primordia and in young nucellus. In *C. wabiske*, it was considered that the shorter the interval between microsporogenesis and megasporogenesis was, the more abnormal anthers and embryo sacs as well as meiosis in PMCs would be observed.

Literature Cited

- CROWDER, L.V., 1953. Interspecific and intergeneric hybrids of *Festuca* and *Lolium*. Jour. Hered. 44: 195~203.
- DAVIS, G.L., 1966. Systematic Embryology of the Angiosperms. p. 217.
- HUTINOUE, Y. and HUTINOUE, H., 1965. Studies on the flowering and fruiting of the tea plant: (in Japanese). Bull. Saitama Tea Exp. Sta. No. 3: 1~33.
- IWAMASA, M., 1966. Studies on the sterility in genus *Citrus* with special reference to seedlessness. Bull. Hort. Res. Sta. Japan Ser. B, No. 6: 1~83.
- KAPIL, R.N. and SETHI, S.B., 1963. Development of male and female gametophytes in *Camellia sinensis* (L.) KUNTZE, O. Proc. Nat. Inst. Sci. India 29 (5): 567~574.
- KIHARA, H., 1951. Substitution of nucleus and its effects on genome manifestations. Cytologia. 16: 177~193.
- KITAMURA, S., 1965. Species relationships in genus *Camellia* (in Japanese). Shin-kaki 45: 40~46.
- SIMURA, T. and OSONE, K., 1956. Studies on the fertilization of the tea plant. Japan. J. Breed. 6: 43~46.
- WHYTE, R.O., 1929. Studies in *Ranunculus*. II. the cytological basis of sex in *R. acris* L. Jour. Gen. 21: 183~191.

ツバキ属植物における細胞遺伝学的研究

I. ワビスケ, ツバキおよびチャの成熟分裂および配偶子形成の比較

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チャの耐凍性品種を得るために、チャとチャ以外のツバキ属植物とを交雑することが多くの人によって行なわれている。ワビスケがチャとツバキの雑種であれば、チャとツバキとの交雑性も大きいと考えられる。したがって、著者らはいろいろの方法でチャとツバキを交雑することを試みているが、ここではまず、ワビスケの減数分裂と胚嚢および葯形成について報告する。

成熟分裂については、ワビスケは品種により異なり、アカワビスケやシロワビスケではチャやツバキと同様に成熟分裂は正常に行なわれ、胚嚢や葯の形成も正常に行なわれた。ところが、スキヤワビスケとウスワビスケでは、成熟分裂に1価染色体が多くみられ、花粉稔性は1価染色体が多いものほど低かった。また、胚嚢と葯形成も異常が多くみられ、コチョウシロワビスケでは、ほとんど葯と胚嚢が形成されなかった。このためワビスケは、品種によって程度の差はあるが、染色体の間に非相同性

があると考えられる。したがって今後核型分析をする必要がある。さらに、葯室形成において、チャ、ヤブツバキ、ワビスケにおいても、壁細胞が平行分裂し、外側の細胞が二層の中間層と内被を、内側の細胞がタペート層を形成し、開花時には、タペート層と中間層は退化していた。

次に、チャでは、胚嚢形成において線状四分子が形成されるといわれてきたが、ツバキ、チャ、ワビスケにおいて、いずれも二分子しか形成されないとみてよいことがわかった。また、ワビスケの中にみられる葯形成と胚嚢形成の異常は、それぞれの始原体が形成されるときに異常がみられ、さらにそれぞれの胞原細胞の分裂の異常によることがわかった。そして、チャやツバキの場合と比較してみるとワビスケの胚嚢形成の時期と葯形成の時期が接近しているものほど、葯や胚嚢に異常の多いことがわかった。