Kasetsart J. (Nat. Sci.) 44 : 536 - 543 (2010)

Meiotic Behavior in Microsporocytes of Some Bananas in Thailand

Therdsak Thonnalak[1], Benchamas Silayoi[1]*,
Yingyong Paisooksantivatana[1] and Pradit Pongtongkam[2]

ABSTRACT

Meiotic behavior was investigated in the microsporocytes of six wild bananas with *AA* and *BB* genomes and 46 cultivated bananas with *AA*, *AAA*, *BBB*, *AAB* and *ABB* genomes. All banana material was collected from the Pak Chong Research Station, Kasetsart University, Nakhon Ratchasima, Thailand. Most of the wild bananas showed normal synapses with a high chromosome pairing frequency of 11 bivalents per pollen mother cell (PMC). The cultivated bananas exhibited many variations in chromosome association at metaphase-I. Cultivars with the *AA* genome had more univalents than those of wild species with the same *AA* genome. Univalent, bivalent and trivalent occurrences were also common in all triploid cultivated bananas, but quadrivalents were very rare. The univalents were high in the *AAB* and *ABB* genomes, whereas trivalency was high in the *AAA* and *BBB* genomes. Micronuclei were observed in the tetrad of all cultivated bananas, but were very low in wild bananas. Many types of tetrad were shown in different orientation patterns at metaphase-II. The occurrence of the parallel disposition pattern was high, but the perpendicular and lineal disposition patterns were not common in any of the bananas.

Keywords: bananas, genome, chromosome, meiotic behavior, microsporocytes

INTRODUCTION

Bananas (*Musa* spp.) are giant perennial herbs that are cultivated in the tropical and sub-tropical regions of the world as staple food and cash crops (Oselebe *et al*., 2006). The genus *Musa* is a member of the Musaceae family. It has 22 chromosomes in the wild species and varies between 22, 33 and 44 chromosomes in cultivated crops, with a basic chromosome number of 11 (Nelson *et al*., 2006; Oselebe *et al*., 2006). The majority of cultivars is triploid and derives from intra-specific crosses within *Musa acuminata* Colla (*A* genome) and inter-specific crosses between *M. acuminata* and *M. balbisiana* Colla (*B* genome) (Silayoi, 2002). The taxonomic nomenclature of cultivated bananas is based on the scoring of fifteen morphological descriptions of *M. balbisiana* and *M. acuminata* for genome constitution and ploidy. The main genomic groups are comprised of *AA, AAA, AAB, AB, AABB, ABB, ABBB* and *BB* (Simmonds and Shepherd, 1955). The *BBB* group, specifically found in Thailand, was added by Silayoi and Babpraserth (1983), in a modified version.

A taxonomic nomenclature based on morphological traits is a traditional and valuable starting point for cytogenetics, as well as molecular genetics. The genomic designations are broadly functional and primarily based on chromosome

---

[1] Department of Horticulture, Faculty of Agriculture, Kasetsart University, Bangkok 10900, Thailand.
[2] Department of Genetics, Faculty of Science, Kasetsart University, Bangkok 10900, Thailand.
* Corresponding author, e-mail: agrbms@ku.ac.th

Received date : 06/01/09 Accepted date : 24/03/10

pairing, rather than evolutionary definition. The degree of chromosome pairing in intra- and inter-specific hybrids provides an important cytogenetic context for inferring phylogenetic relationships among species, enhances the understanding of evolution of the genus and provides information about the ancestral species. Genomic groups are correlated typically with the evolutionary group. Therefore, the taxonomic nomenclature of the species and evolutionary relationships can be refined by cytogenetic evidence (Singh, 2003).

A comprehensive summary of meiotic studies in *Musa* was given by Shepherd (1999). Wild species were found to show regular chromosome pairing with 11 bivalents. On the other hand, diploid, triploid or tetraploid parthenocarpic clones showed aberrant chromosome pairing with univalents, trivalents and multivalents, indicating heterozygosity for one or more translocations or inversions (Agarwal, 1983; Shepherd, 1999). This information is important for mapping studies, as chromosomal structural changes may influence recombination and affect the interpretation of results (Doležel, 2004).

This investigation of meiotic behavior could distinguish the chromosome association of cultivated bananas to wild species in Thailand.

MATERIALS AND METHODS

Collections were made from the Pak Chong Research Station, Kasetsart University, Nakhon Ratchasima, Thailand of the flower buds of 3 wild *M. acuminata* (Kluai Pa Phare, Kluai Pa Pli Som and Kluai Pa Pli Lueang), 3 wild *M. balbisiana* (Kluai Tani Eisan, Kluai Tani Nua and Kluai Tani Tai), 11 cultivars with *the AA* genome (Kluai Khai, Kluai Kasetsart Banana 2, Kluai Kasetsart Banana 3, Kluai Khai Thong Ngeoy, Kluai Khai Thong Roung, Kluai Leb Mu Nang, Kluai Hom Chan, Kluai Sa, Kluai Hom Champa, Kluai Thong Khi Maew, and Kluai Hom Son), 9 cultivars with the *AAA* genome (Kluai Hom Thong, Kluai Hom Khieo, Kluai Hom Khieo Khom, Kluai Hom Karen, Kluai Khai Pra Tabong, Kluai Nak, Kluai Krang, Kluai Nam Nom and Kluai Nam Thai), 4 cultivars with the *BBB* genome (Kluai Hin, Kluai Lep Chang Kut, Kluai Phama Heak Kuk and Kluai Saba), 11 cultivars with the *AAB* genome (Kluai Chin, Kluai Khom, Kluai Khai Boran, Kluai Nam, Kluai Nam Kab Dam, Kluai Nam Phad, Kluai Nang Paya, Kluai Roi Wi, Kluai Nom Sao, Kluai Nue Mu Nang and Kluai Nue Jorakhe) and 11 cultivars with the *ABB* genome (Kluai Hak Muk Khao, Kluai Hak Muk Khieo, Kluai Namwa Dam, Kluai Namwa Dang, Kluai Namwa Khao, Kluai Namwa Khom, Kluai Namwa Lueang, Kluai Namwo, Kluai Nom Mi, Kluai Som and Kluai Tip).

Each flower bud of about 2.0 inch in length was fixed for 48 h in Carnoy’s solution of ethanol-acetic acid (3:1) at room temperature and kept in 70% ethanol at 4℃ until used. Fixed anthers were rinsed in distilled water before use. Each anther was transferred to a clean slide and excessive water was removed. Then, the anther was squashed and stained with 1% aceto-carmine. Finally slides were sealed and examined under an OLYMPUS CH-2 light microscope.

RESULTS

The meiotic division in the microsporocytes of 3 wild *M. acuminata*, 3 wild *M. balbisiana* and 46 cultivated bananas in several genome groups were studied. Observation of meiosis among this material is summarized in Table 1. All wild bananas of both *M. acuminata* and *M. balbisiana* exhibited normal synapses with a frequency of 11 bivalents per pollen mother cell (PMC) (Figures 1a-f). The frequency of univalents in microsporogenesis was 0.1 in Kluai Pa Pli Som and Kluai Tani Tai, 0.4 in Kluai Tani Eisan per PMC, but no univalency was shown in Kluai Pa Phare and Kluai Pa Pli Lueang. The diploid cultivars with the *AA* genome showed 10.0 and 10.8 bivalents per PMC in Kluai Kasetsart Banana 3 and Kluai Hom Champa, respectively. The univalency in microsporogenesis was quite low in Kluai Hom Champa and Kluai Thong Khi Maew, but high in the other *AA* cultivars, such as Kluai Kasetsart Banana 2, Kluai Kasetsart Banana 3, Kluai Leb Mu Nang and Kluai Hom Chan.

The meiotic behavior in the microsporocytes of the triploid cultivated bananas exhibited many variations in chromosome association in metaphase-I (Figures 2 and 3). The bananas with the *AAA* genome showed frequencies of 3.4 and 5.1 trivalents per PMC in Kluai Nam Thai and Kluai Nak, Kluai Nam Nom, respectively. The *AAA* genome also showed 4.3 and 6.8 univalents per PMC in Kluai Nam Nom and Kluai Nam Thai, respectively. Quadrivalency was found only in Kluai Hom Khieo and Kluai Hom Khieo Khom, with a frequency of 0.1. The univalency in microsporogenesis of Kluai Lep Chang Kut was 4.7 per PMC, which was the lowest in the *BBB* group. The frequency of bivalents per PMC in the *BBB* bananas was 6.5 in Kluai Lep Chang Kut and 7.3 in Kluai Hin. Trivalency was found also at metaphase-I in all the *BBB* cultivars, with the highest being 5.1 trivalents per PMC in Kluai Lep Chang Kut.

The cultivated bananas in the *AAB* genome exhibited variations in chromosome pairing, having frequencies of bivalency per PMC of 6.4 in Kluai Roi Wi and of 7.6 in Kluai Khom. Trivalency was also common in all the *AAB* bananas showing frequencies of 2.8 per PMC in Kluai Nam Phad and 3.8 per PMC in Kluai Khai Boran. The cultivated bananas with *ABB* showed bivalent frequencies per PMC of 6.3 in Kluai Namwo and 7.7 in Kluai Namwa Dam and Kluai Namwa Lueang. The trivalents per PMC were 2.9 in Kluai Hak Muk Khieo and 3.8 in Kluai Tip. The bivalents per PMC in both *AAB* and *ABB* bananas were lower than those of the wild species, but univalency was higher than in the wild ones. The frequency of univalents per PMC was 7.4 in Kluai Namwa Lueang and 10.5 in Kluai Nam Phad. The only quadrivalent in microsporogenesis was 0.1 in Kluai Nang Paya (Table 1).

The micronucleus was the result of abnormal chromosome segregation. The microsporocytes were originated by extra cytokinesis and it could be observed from tetrad microsporocytes (Figures 4a-c). The tetrad showed a micronucleus in all triploid bananas, (8% in Kluai Lep Chang Kut and 22% in Kluai Nom Sao, Kluai Hak Muk Khao and Kluai Tip). The micronucleus occurrence was low in wild bananas and diploid cultivars (Table 1).

The spindle fiber had different orientation patterns during metaphase II. The parallel disposition (Figure 4d), which is a common pattern in all metaphases of normal meiosis, occurred in 96-100% of wild bananas, 90- 98% in diploid cultivated bananas and 78-94% in triploid cultivars. The perpendicular and lineal dispositions, which are abnormal patterns, had a low occurrence in all bananas (Table 1 and Figures 4e, f).

DISCUSSION

The meiotic behavior of cultivated bananas with the *AA* genome showed more univalency than the wild species. This phenomenon has previously been observed in some Thai bananas with the *AA* genome (Pupittayasathaporn, 1974). This behavior could be due to non-homology between the *A* genomes of both parents. Similar results were obtained from the molecular studies leading to the classification of Thai *acuminata* bananas into three genome groups of A_1A_1 in Kluai Pa Phrae, A_2A_2 in Kluai Hom Champa and A_1A_2 in certain hybrid cultivars of Kluai Khai (Phothipan *et al.*, 2006). Therefore, the Kluai Hom Chan, Kluai Thong Khi Maew, Kluai Hom Son, Kluai Sa, Kluai Khai Thong Roung and Kluai Khai Thong Ngeoy should also be hybrids between A_1 and A_2, due to the similar univalency found. However, the greater amount of univalency observed in Kluai Kasetsart Banana 2 and Kluai Kasetsart Banana 3 than in Kluai Khai suggested that some mutation must have occurred in Kluai Khai that resulted in these two new cultivars (Silayoi, 2002).

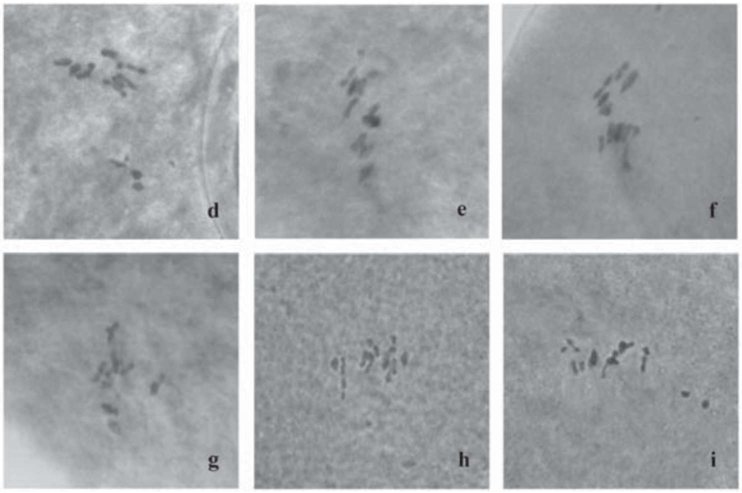

Figure 1 Microscopic photographs of different banana species showing meiotic behavior at metaphase-I: a) Kluai Pa Phare 11 II; b) Kluai Pa Pli Som 2 I+10 II; c) Kluai Pa Pli Lueang 11 II; d) Kluai Tani Eisan 11 II; e) Kluai Tani Nua 2 I+10 II; f) Kluai Tani Tai 11 II; g) Kluai Hom Champa 11 II; h) Kluai Kasetsart Banana 2 2 I+10 II; and i) Kluai Hom Son 4 I+9 II (7,500X).

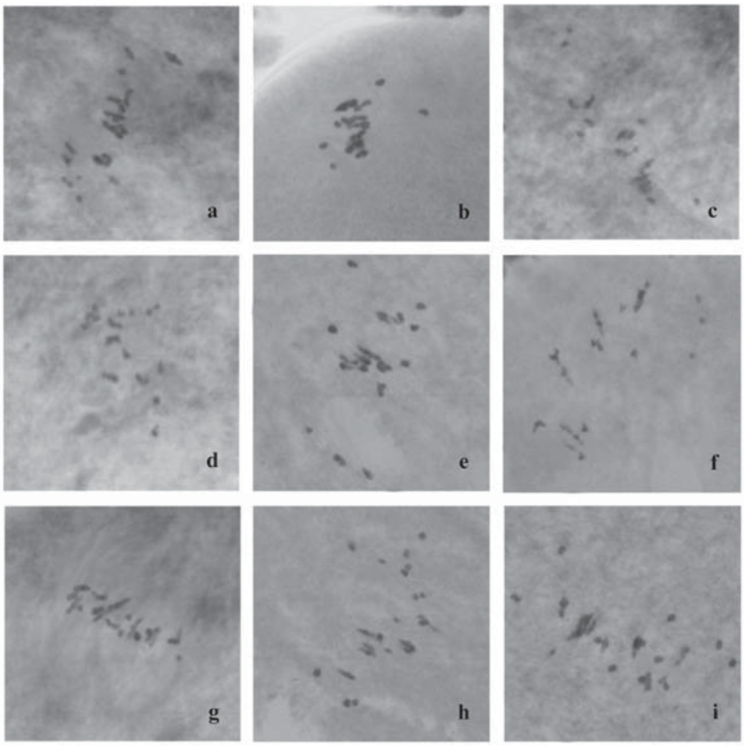

Figure 2 Microscopic photographs of different banana species showing meiotic behavior at metaphase-I: a) Kluai Hin 4 I+10 II+3 III; b) Kluai Lep Chang Kut 5 I+8 II+4 III; c) Kluai Phama Heak Kuk 2 I+11 II+3 III; d) Kluai Saba 2 I+11 II+3 III; e) Kluai Hom Thong 4 I+10 II+3 III; f) Kluai Hom Khieo 4 I+7 II+5 III; g) Kluai Hom Khieo Khom 4 I+10 II+3 III; h) Kluai Nak 13 I+7 II+2 III; and i) Kluai Nam Thai 10 I+7 II+3 III (7,500X).

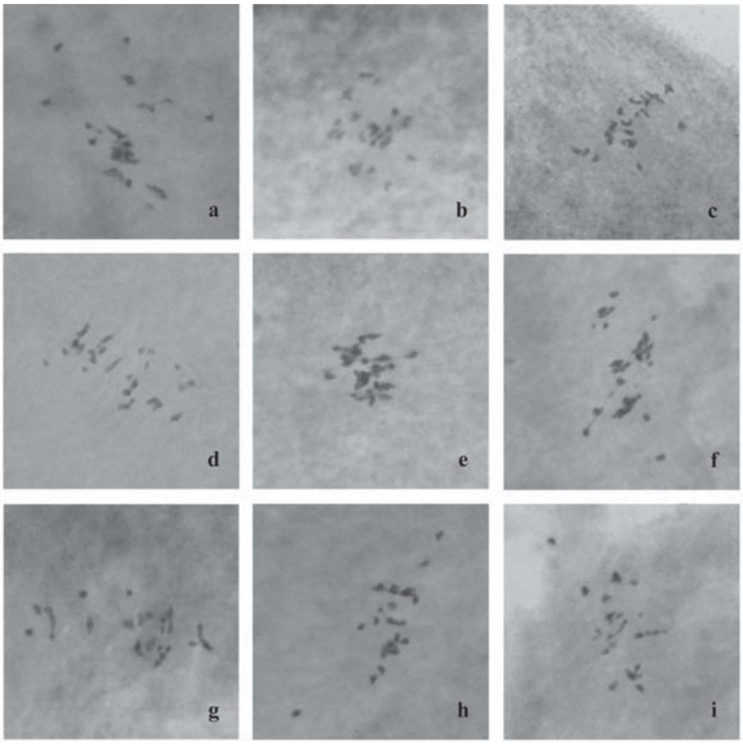

Figure 3 Microscopic photographs of different banana species showing meiotic behavior at metaphase-I: a) Kluai Chin 7 I+10 II+2 III; b) Kluai Khom 3 I+12 II+2 III; c) Kluai Nang Paya 4 I+10 II+3 III; d) Kluai Roi Wi 8 I+11 II+1 III; e) Kluai Hak Muk Khao 3 I+12 II+2 III; f) Kluai Namwa Dam 6 I+12 II+1 III; g) Kluai Namwa Lueang 4 I+10 II+3 III; h) Kluai Nom Mi 5 I+11 II+2 III; and i) Kluai Tip 8 I+8 II+3 III (7,500X).

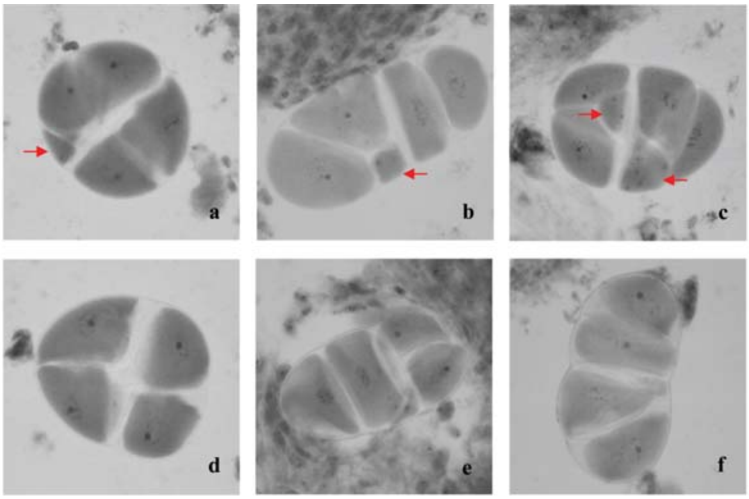

Figure 4 Microscopic photographs of different banana species showing types of tetrad of: a) Kluai Lep Chang Kut; b) a tetrad with a small micronucleus (arrow); c) a tetrad with two micronuclei (arrows); d) spindle in parallel disposition producing a normal tetrad; e) perpendicular disposition; and f) lineal disposition (1,400X).

Table 1 Chromosome association at meiosis in microsporocytes of some bananas in Thailand.

No.	Varietyies[a]	2n	No. of PMC	Frequencies of chromosome paring per PMC				Tetrad with micronuclei (%)	Type of tetrad (%)		
				I	II	III	IV		Parallel	Perpendicular	Lineal
Wild *M. acuminata*											
1.	Kluai Pa Phare	22	20	0	11	0	0	2	96	2	2
2.	Kluai Pa Pli Som	22	20	0.1	10.9	0	0	2	96	4	0
3.	Kluai Pa Pli Lueang	22	20	0	11	0	0	0	98	0	2
Wild *M. balbisiana*											
4.	Kluai Tani Eisan	22	20	0.4	10.8	0	0	2	98	2	0
5.	Kluai Tani Nua	22	20	0.3	10.8	0	0	0	98	2	0
6.	Kluai Tani Tai	22	20	0.1	10.9	0	0	0	100	0	0
Cultivars within *AA* genome											
7.	Kluai Khai	22	20	1.8	10.1	0	0	2	92	4	4
8.	Kluai Kasetsart Banana $_2$	22	20	2.0	10.1	0	0	4	96	4	0
9.	Kluai Kasetsart Banana $_3$	22	20	2.0	10.0	0	0	2	94	4	2
10.	Kluai Khai Thong Ngeoy	22	20	1.7	10.2	0	0	4	92	4	4
11.	Kluai Khai Thong Roung	22	20	1.7	10.2	0	0	2	98	2	0
12.	Kluai Leb Mu Nang	22	20	1.9	10.2	0	0	4	96	0	4
13.	Kluai Hom Chan	22	20	1.9	10.4	0	0	4	92	6	2
14.	Kluai Sa	22	20	1.7	10.3	0	0	2	94	6	0
15.	Kluai Hom Champa	22	20	0.5	10.8	0	0	0	96	2	2
16.	Kluai Thong Khi Maew	22	20	0.7	10.7	0	0	0	98	2	0
17.	Kluai Hom Son	22	20	1.6	10.3	0	0	4	90	8	2
Cultivars within *AAA* genome											
18.	Kluai Hom Thong	33	20	6.0	6.3	4.8	0	18	84	6	10
19.	Kluai Hom Khieo	33	20	5.4	6.7	4.6	0.1	14	78	12	10
20.	Kluai Hom Khieo Khom	33	20	6.0	6.1	4.8	0.1	14	86	8	6
21.	Kluai Hom Karen	33	20	6.3	6.5	4.5	0	16	88	6	6
22	Kluai Khai Pra Tabong	33	20	5.9	6.2	5.0	0	10	80	8	12
23	Kluai Nak	33	20	4.6	6.5	5.1	0	12	84	10	6
24.	Kluai Krang	33	20	5.3	6.7	4.9	0.1	16	86	8	6
25.	Kluai Nam Nom	33	20	4.3	6.7	5.1	0	16	86	8	6
26.	Kluai Nam Thai	33	20	6.8	7.4	3.4	0	14	88	4	8

Table 1 Chromosome association at meiosis in microsporocytes of some bananas in Thailand.

No.	Varietyies[a]	2n	No. of PMC	Frequencies of chromosome paring per PMC				Tetrad with micronuclei (%)	Type of tetrad (%)		
				I	II	III	IV		Parallel	Perpendicular	Lineal
Cultivars within *BBB* genome											
27.	Kluai Hin	33	20	7.8	7.3	3.6	0	20	88	8	4
28.	Kluai Lep Chang Kut	33	20	4.7	6.5	5.1	0	8	92	4	2
29.	Kluai Phama Heak Kuk	33	20	8.7	6.9	3.3	0	16	88	6	6
30.	Kluai Saba	33	20	6.7	7.0	4.1	0	18	86	10	4
Cultivars within *AAB* genome											
31.	Kluai Chin	33	20	9.1	7.2	3.2	0	20	82	10	8
32.	Kluai Khom	33	20	8.5	7.6	3.1	0	18	88	8	4
33.	Kluai Khai Boran	33	20	8.7	6.5	3.8	0	18	84	6	10
34.	Kluai Nam	33	20	9.7	7.1	3.0	0	20	88	6	6
35.	Kluai Nam Kab Dam	33	20	9.9	7.0	3.3	0	18	80	14	6
36.	Kluai Nam Phad	33	20	10.5	7.0	2.8	0	14	86	6	8
37.	Kluai Nang Paya	33	20	8.0	7.2	3.4	0.1	18	88	6	6
38.	Kluai Roi Wi	33	20	10.0	6.4	3.4	0	16	90	2	8
39.	Kluai Nom Sao	33	20	9.5	7.2	3.0	0	22	84	8	8
40.	Kluai Nue Mu Nang	33	20	7.9	7.0	3.7	0	20	82	10	8
41.	Kluai Nue Jorakhe	33	20	9.6	7.2	3.0	0	18	86	10	4
Cultivars within *ABB* genome											
42.	Kluai Hak Muk Khao	33	20	8.4	6.9	3.6	0	22	84	8	8
43.	Kluai Hak Muk Khieo	33	20	9.1	7.6	2.9	0	20	86	10	4
44.	Kluai Namwa Dam	33	20	8.1	7.7	3.2	0	18	86	8	6
45.	Kluai Namwa Dang	33	20	8.4	7.3	3.3	0	14	82	12	6
46.	Kluai Namwa Khao	33	20	10.0	6.5	3.3	0	16	88	6	6
47.	Kluai Namwa Khom	33	20	7.5	7.2	3.7	0	18	88	8	4
48.	Kluai Namwa Lueang	33	20	7.4	7.7	3.4	0	14	86	10	4
49.	Kluai Namwo	33	20	9.8	6.3	3.4	0	20	86	6	8
50.	Kluai Nom Mi	33	20	8.8	7.1	3.3	0	18	86	10	4
51.	Kluai Som	33	20	8.6	7.4	3.3	0	18	94	4	2
52.	Kluai Tip	33	20	8.6	7.9	3.8	0	22	86	8	6

PMC = pollen mother cell, I = univalent, II = bivalent, III = trivalent, IV = quadrivalent.

[a] = genome classification by Silayoi and Babpraserth (1983) except No. 8 and 9

In the current study results, the autotriploids of 11 trivalents were not observed in the *AAA* or *BBB* groups. Instead, different numbers of univalents, bivalents and trivalents were found in these groups. The occurrence of univalents was also observed in some Thai bananas with the *AAA* genome (Pupittayasathaporn, 1974). Univalency in autotriploid cultivars is known generally to be the result of the absent chiasmata. This behavior would imply that there must be an abnormal spindle that leads to micronucleus formation and the loss of chromatin. The high percentage of univalent chromosomes exhibited in triploid bananas with the *AAA* and *BBB* genomes could be due either to non-homology or genetic recombination between the genomes of both parents. Similar meiotic abnormalities were also found in intra-specific hybrids in *Oryza* (Lu *et al.*, 1997). In the current study, bivalency and trivalency were very common in autotriploid bananas, as was found in Kluai Hom Thong, Kluai Hom Khieo, Kluai Hom Khieo Khom, Kluai Hom Karen, Kluai Khai Pra Ta Bong, Kluai Nak, Kluai Krang, Kluai Nam Nom, Kluai Nam Thai, Kluai Hin, Kluai Lep Chang Kut, Kluai Phama Heak Kuk and Kluai Saba. On the other hand, quadrivalency was observed in Kluai Hom Khieo and Kluai Hom Khieo Khom with a frequency of 0.1. This same frequency was also reported by Shepherd (1999) in some *AAA* and *AAB* groups of bananas. The occurrence of quadrivalents might be regarded as further evidence of disturbances in the homologies of the chromosome segments. The associations of the four chromosomes have been speculated to be the results of either simple and reciprocal eucentric translocation or duplication, or both (Dodds, 1943).

For the allotriploid bananas, the current results for the *AAB* and *ABB* genomes showed more complicated chromosome associations, especially with univalents and multivalents. The chances of observing the genomic constitution of these cultivars as 11 univalents and 11 bivalents were very low. Udompongsanon (1969) suggested that meiotic behavior could differentiate chromosome *A* from the *B* genome, but the detection of potential inter-specific intra-chromosomal exchanges could not be clearly seen, because of the limitations in the chromosomal technique used. Moreover, due to the nature of the *Musa* chromosome, that is, the small size, the similarity of chromosome morphology and the non-uniformity of contraction identification, the discrimination of the *A* and *B* genomes, using conventional cytological methods is difficult (Osuji *et al.*, 1997). However, the findings of the current study were similar to phenomena previously observed in diploid hybrid bananas (Dodds, 1943; Shepherd, 1999), polyploidy hybrids (Dodds and Simmonds, 1946) and in some allotriploid Thai bananas (Udompongsanon, 1969; Pupittayasathaporn, 1974). It was the same phenomena found in meiotic abnormalities that were present also in inter-specific hybrids in other plants, such as *Oryza* (Mariam *et al.*, 1996) and *Brachiaria* (Adamowski *et al.*, 2008).

The findings of micronuclei and abnormal tetrads in cultivated bananas were more complicated than those in wild species. Souza *et al.* (1997) and Bajpai and Singh (2006) indicated that more meiotic abnormalities would produce more abnormal tetrads, as is clearly shown in *Brassica* spp. and papaya. The prophase-I of papaya apparently showed abnormalities because of low chiasmata or due to the presence of asynaptic genes (Bajpai and Singh, 2006). In the results of the current study, the spindle fibers were seen in different orientation patterns during metaphase-II, contrary to the parallel disposition, which is the common pattern in all metaphases of the normal meiosis in bananas. In some cells of banana cultivars, convergent, perpendicular and lineal patterns could be found. These are abnormal patterns, which lead to sterile cultivars. During metaphase-I, incorrect chromosome orientation might accumulate the microtubules around the separated chromosomes to form spindle fibers in the meiotic cells. This behavior is similar to that described in some Thai bananas by Pupittayasathaporn (1974) and also in rice by Sanabria *et al*. (2006).

The current paper has described the use of meiotic behavior to distinguish the ploidy in diploid, autotriploid and allotriploid bananas. The chromosome association and tetrad types were observed and revealed that the high ploidy of bananas resulted in high abnormalities in meiosis. These findings showed the non-homology of the chromosomes in the *A* and *B* genomes and would be good background information for further molecular work.

CONCLUSION

1. Wild bananas exhibited normal synapses in metaphase-I.
2. The cultivars with the *AA* genome showed more univalency than did wild species.
3. The bananas with the *AAA* genome and Kluai Lep Chang Kut with the *BBB* genome exhibited greater trivalency than bananas in other genomes.
4. Univalency was shown in the *AAB* and *ABB* genomes more than in the *AAA* and *BBB* genomes.
5. A micronucleus was observed in the tetrad microsporocytes of all cultivated bananas, but this occurrence was very low in wild bananas.
6. The parallel disposition pattern of tetrads occurred in high numbers, but the perpendicular and lineal patterns were low.

ACKNOWLEDGEMENTS

The authors are most grateful to the Pak Chong Research Station, Kasetsart University, Nakhon Ratchasima for providing plant material and the Department of Horticulture, Faculty of Agriculture, Kasetsart University, Bangkok for the use of the cytological laboratory.

LITERATURE CITED

Adamowski, E.D.V., M.S. Pagliarini and C.B.D. Valle. 2008. Meiotic behavior in three interspecific three-way hybrids between *Brachiaria ruziziensis* and *B. brizantha* (Poaceae: Paniceae). **J. Genet.** 87(1): 33-38.

Agarwal, P.K. 1983. Cytogenetical investigations in Musaceae. I. Meiotic studies in South Indian bananas. **Cytologia** 48: 847-852.

Bajpai, A. and A.K. Singh. 2006. Meiotic behavior of *Carica papaya* L.: spontaneous chromosome instability and elimination in important cvs. in North India conditions. **Cytologia** 71(2): 131-136.

Dodds, K.S. 1943. Genetical and cytological studies of *Musa*. V. Certain edible diploid. **J. Genet.** 45: 113-138.

Dodds, K.S. and N.W. Simmonds. 1946. Genetical and cytological studies of *Musa*. VIII. The formation of polyploid spores. **J. Genet.** 47(3): 223-241.

Doležel, J. 2004. Cytogenetic and cytometric analysis of nuclear genome in *Musa*, pp. 245-249. *In* S.M. Jain and R. Swennen (eds.). **Banana Improvement: Cellular, Molecular Biology and Induced Mutations**. Science Publishers, Inc., New Hampshire.

Lu, B.R., M.E.B. Naredo, A.B. Juliano and M.T. Jackson. 1997. Hybridization of *AA* genome rice species from Asia and Australia II. Meiotic analysis *Oryza meridionalis* and its hybrids. **Genet. Resour. Crop Evol.** 44(1): 25-31.

Mariam, A.L., A.H. Zakri, M.C. Mahani and M.N. Normah. 1996. Interspecific hybridization of cultivated rice, *Oryza sativa* L. with the wild rice, *O. minuta* Presl. **Theor. Appl Genet.** 93: 664-671.

Nelson, S.C., R.C. Ploetz and A.K. Kepler. 2006. *Musa* species (bananas and plantains), ver. 2.2., pp. 583-615. *In* C.R. Elevitch (ed.). **Species Profile for Pacific Island Agroforestry**. Permanent Agriculture

Resources, Hawaii.

Oselebe, H.O., A. Tenkouano and M. Pillay. 2006. Ploidy variation of *Musa* hybrids from crosses. **Afr. J. Biotechnol.** 5(11): 1048-1053.

Osuji, J.O., G. Harrison, J. Crouch and J.H. Heslop-Harrison. 1997. Identification of the genomic constitution of *Musa* L. lines (bananas, plantains and hybrids) using molecular cytogenetics. **Ann. Bot.** 80: 787-793.

Phothipan, S., B. Silayoi, K. Wanichkul and S. Apisitwanich. 2006. Genetic relationship among bananas in *AA*, *AAB* and *BB* Groups Using Random Amplified Polymorphic DNA (RAPD) and Sequence Related Amplified Polymorphism (SRAP) Techniques. **Kasetsart J. (Nat Sci.)** 39(4): 703-710.

Pupittayasathapron, A. 1974. **Cytological Investigation in Some Banana Clones**. M.S. thesis, Kasetsart University, Bangkok.

Sanabria, Y., C. Olaya, J. Carabali, C.M. Caetano, C. Martinez and J. Tohme. 2006. Chromosome elimination in the diploid *Oryza sativa* L. x tetraploid *O. latifolia* Desv. **Annual Report 2006**. 12-24.

Shepherd, K. 1999. **Cytogenetics of the Genus *Musa*.** INIBAP, Montpellier. 160 pp.

Silayoi, B. and C. Babpraserth. 1983. **Banana Genetic Resources Exploration in Thailand**. Report, Submitted to IBPGR, Kasetsart University, Bangkok. 131 pp.

Silayoi, B. 2002. **Banana**. 3rd ed. Kasetsart University Publ., Bangkok. 357 pp.

Singh, R.J. 2003. **Plant Cytogenetics**. 2nd ed. CRC press LLC, New York. 488 pp.

Simmond, N.W. and K. Shepherd. 1955. The taxonomy and origins of cultivated bananas. **J. Linn. Soc. (Bot.)** 55: 302-312.

Souza, A.M., M.S. Pagliarini, J.U.T. Brandao-Filho, I.M. Carraro and L.C. Balbino.1997. Evaluation of meiotic behavior in canola (*Brassica napus* var. *oleifera* and *Brassica Campestris* var. *oleifera*) cultivars recently introduced in Brazil. **Nucleus** 40: 95-100.

Udompongsanon, P. 1969. **The Botanical Study on Some Bananas of Thailand**. M.S. thesis, Kasetsart University, Bangkok.