

INTRA-INDIVIDUAL VARIATION IN NUMBER OF  
B CHROMOSOMES IN *MISCANTHUS*  
*JAPONICUS* ANDERSS.<sup>(1)</sup>

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(Received June 6, 1961)

In the fall of 1955, Dr. H. W. Li and his colleagues of the Taiwan Sugar Experiment Station collected 197 clones of *Miscanthus japonicus* Anderss. from various parts of its distributing area in Taiwan. Originally this was a part of Dr. Li's project for looking into the cytogenetics of sugarcane and its relatives. It happened, however, that four out of the 197 clones had varying number of B, or accessory, chromosomes in addition to the normal complement,  $2n=38$  (Li, *et al.*, 1950). The collection numbers of those clones were: Wu-lai 1, Wu-lai 13, Ta-wu 23 and Ta-wu 47. Morphologically these clones did not differ from the others.

The above-mentioned material was put to the present writer's disposal by Dr. Li in the summer of 1960. But at that time there were only two clones available, Ta-wu 47 and Wu-lai 13; Wu-lai 1 had died out during propagation, while Ta-wu 23 was mixed up with other clones that were free from B chromosomes. Therefore, this work is concerned mainly with clones Wu-lai 13 and Ta-wu 47, with particular emphasis laid on the latter, though some studies made by Dr. Li will be reported together.

There was found in these clones a remarkable intra-individual variation in the number of B chromosomes. Not only did the number vary from cell to cell at meiosis, but it was also not constant in the root-tip cells. However, the range of numerical variation was by far greater in the PMC's than in the root-tip cells as will be reported later. In this connection, considerations were made aiming at ascertaining the probable sequence of events which led to the numerical change of B chromosomes as existed in this grass species.

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### Methods

For studying meiosis, young panicles were fixed with 1:3 acetic-alcohol. The fixation of root-tips, taken from divided tillers grown in pots, was made by the modified Wärmke's method (Li *et al.*, 1955). In both cases, the fixed materials were studied by acetocarmine squash technique.

Each spikelet of this species contains three anthers. In the beginning of this work, slides were made on a one-spikelet-to-one-slide basis, PMC's from the three anthers being mounted together in a slide. Later, in order to find out the numerical variation of B chromosomes in more detail, the three anthers in the same spikelet were separated and each mounted on a slide.

For analysis of variance of the data, formulas were constructed following the method of hierarchical classification (Kempthorne, 1952) with four ranks of unequal numbers, *i.e.*, the panicle, the branch, the spikelet and the anther. They are given in the Appendix.

### Cytological Observation

1. *The Normal Chromosome Complement.* Studies of root-tip cells in clone Ta-wu 47 showed that there were 38 chromosomes mostly having median or submedian centromeres (Figs. 1 & 2). They formed 19 bivalents at meiosis, all of which showed regular disjunction. Bridge-like structures at AI (Fig. 10), though extremely rare, were the only irregularity found in this clone.

2. *The B Chromosomes.* In the metaphase plate of root-tip cells, the B chromosomes appeared as small dots about 1/3 times as large as the shortest chromosome of the regular complement, and were apparently heterochromatic (Figs. 1 & 2). At pachynema, in Ta-wu 47, two types were recognized in the B chromosomes: One had a sub-median centromere, and the other, about half of the former in length, seemed to have a median centromere (Figs. 3 & 4). However, they could hardly be distinguished from each other in the metaphase plates of root-tips (Figs. 1 & 2). At diakinesis and MI, the majority of the B chromosomes appeared as univalents, while the rest formed bivalents. In a few instances trivalents or tetravalents were found at diakinesis (Fig. 5 & Table 1). Nevertheless, no higher associations than bivalents were observed at MI (Figs. 6 & 7). Pairing of the B chromosomes with members of the normal complement was never found at diakinesis nor at MI. The frequencies of various meiotic configurations of the B chromosomes are given in Table 1. The B univalents did not usually congress onto the metaphase plate but lay mostly at its periphery. At AI they were as a rule distributed at random into the polar spheres without division, and become included into the daughter nuclei.

Table 1. Frequencies of PMC's with various configurations of B chromosomes at diakinesis (top) or MI (bottom), scored in clone Ta-wu 47 (1960).

19A <sub>II</sub> * ↓ →	Num. of B univalent (B <sub>I</sub> )											
	0	1	2	3	4	5	6	7	8	9	10	
Num. of B bivalent (B <sub>II</sub> )	0	3 26	25 120	139 120	214 125	318 253	141 61	91 44	35 20	15 8	6	2
	1	3 3	11 8	24 11	8 4	8 4	6 1	6 3	2	3		
	2	1		1			2	1				
	3	1										
Num. of B trivalent (B <sub>III</sub> )	0											
	1		1									

\* The 19 regular bivalents to which the B univalents (B<sub>I</sub>) and the associated B's (B<sub>II</sub>, B<sub>III</sub>) are to be added from the two directions. For example, the frequency of the chromosome configuration 19A<sub>II</sub>+2B<sub>II</sub>+5B<sub>I</sub> is located in the quadrangle where row 2B<sub>II</sub> and column 5B<sub>I</sub> meet, *i. e.*, 2.

However, the meiotic elimination of the B univalents was by no means moderate: In Ta-wu 47, about one half of the PMC's showed laggards at AI or micronuclei at interphase (Table 2; Figs. 8, 9 & 11). The B bivalents behaved normally at the first meiosis, though they often tended to divide earlier than the members of the regular complement (Fig. 7).

Table 2. Frequencies of PMC's with laggards or micronuclei, scored in clone Ta-wu 47 (1960).

Num. of laggards or micronuclei	0	1	2	3	4	5	Total
Num. of PMC's at AI	5	3	3	2			13
Num. of PMC's at interphase	38	17	3	1		1	60
Total	43	20	6	3		1	73

In Ta-wu 47, efforts were paid to ascertain whether or not somatic non-disjunction of the B chromosomes occurred, but no such phenomena were recognized.

3. *Frequency Distribution of B Chromosomes within Clone.* Chromosome counts were for the most part made at diakinesis and MI. Only figures that permitted clear recognition of the 19 pairs of normal chromosomes as well as the B's were used for taking records. The data obtained showed that the number of B chromosomes per PMC was not constant within a clone or an individual.

In Wu-lai 13, the PMC's showed one or no B chromosome (Table 3). In clones Wu-lai 1, Ta-wu 23 and Ta-wu 47, there were much wider ranges of variation in the number of B's (Tables 3 & 4). Regarding the pattern of variation, these three clones seemed to form another category in contrast to Wu-lai 13. For example, in Ta-wu 47, the number of B's per PMC varied from 0 up to 10, and the mean numbers for anther, spikelet and branch also varied from one to another. As shown in Table 4, frequency distributions for anthers were mostly unimodal, but sometimes appeared to be bimodal or multimodal. The pooled frequencies of various cell classes are listed at the bottom of Table 4, which show a distribution slightly skewed to the left with mode=4 and mean=3.96.

Table 3. Frequencies of B chromosomes in the floral parts of clones Wu-lai 13 (1958), Wu-lai 1 (1956) and Ta-wu 23 (1956).

Clone No.	Spikelet No. (Slide No.)	Num. of PMC's with respective num. of B's										Total	
		0	1	2	3	4	5	6	7	8	9		10
Wu-lai 13	1	35	28										63
	2	26	7										33
	Total	61	35										96
Wu-lai 1		1	3	9	16	5	12	8	7	2		4	64
Ta-wu 23	1		1	4	9	12	11	7	10	4	3	1	62
	6	43	32	35	20	5	3	1					139
	Total	43	33	39	29	17	14	8	10	4	3	1	201

Table 4. Frequency distribution of B chromosomes in the floral parts of clone Ta-wu 47 (1960).

Panicle No.	Branch No.	Spikelet No.	Anther No. (Slide No.)	Num. of PMC's with respective num. of B's.											Total num. of PMC's	Anther mean**	Spikelet mean	Branch mean	Panicle mean
				0	1	2	3	4	5	6	7	8	9	10					
1	1	8	1 2 1	3		4	5	4	3	8*	7	1	5*	32	5.97	6.76	6.76		
																			13
	2	5	1 2 1	3	10	16*	6	4	1	2	7	2	14*	10	40	8.08	5.53	5.53	
	3	2	1 1	3	12	21*	6	4	5	5					50	2.82	2.82	2.82	
	4	6	1 1	3	10	15*	3								30	1.77	1.75	2.35	
	5	1	2 1	3	14*	2	6	15*	3						30	3.47	3.47	3.46	3.87
30																			
6	16	1 1	3	7	7	7	19*	2	4	4	1			35	3.46	3.46	3.46		
																			30
7	3	2 2	3	4	9*	5	4	4	4					18	2.72	3.65	3.66		
																			35
8	8	2 2	3	10*	8	6	6	11	7	1	1			26	2.69	3.67	3.64	3.64	
																			45
9	3	1 1	3	7	13*	10	10	4	4	3	8	9*	8	35	3.40	3.64	3.64		
																			32
9	4	1 1	3	7	6	18*	7	1	1	1	4			40	3.80	3.80	3.91		
																			35
2	1	24	2 3		3	8	9*	3	4	2	1			40	4.38	4.36	4.10		
																			30
	2	28	1 2	3	7	6*	6*	2	3	3	1			30	4.47	3.52	4.42	4.07	
																			17
	2	21	1 1	3	1	5	10*	2	6	6	8	8	1	27	3.59	4.44	4.40	4.08	
																			41
	3	3	1 1	3	12	15*	9*	8	9*	4	4	1		35	5.26	4.40	3.30	3.30	
																			30
	4	21	1 1	3	1	8	9*	8	9*	4	1			40	4.80	4.80	4.08		
40																			3.35
5	32	1 1	3	10*	6	22*	1	1	4				40	3.30	3.30	3.30			
																		40	4.33
5	32	1 2	3	5	9	23*	3	4					40	3.60	3.91	3.91			
																		40	3.60
3	1	11	2 3	12	14*	7	6	6	2	1				39	2.18	2.92	3.77		
																			45
	2	22	1 1	7	11	14*	10	8	1	11	12*	10	2	25	3.16	4.93	3.19	3.98	
																			40
	2	16	2 1	1	15*	12	7	2	3	3	1			40	3.08	3.04	3.35	4.61	
																			50
	3	17	2 2	1	7	14*	5	4	3	1				30	3.20	3.35	4.58	4.15	
																			40
	4	20	1 1	2	4	13	16*	5	2	10	6	3	3	40	3.70	5.25	3.31	4.58	
45																			4.58
4	21	1 1	2	7	11	14*	5	1	1				35	4.57	5.25	3.40	4.15		
																		41	5.63
4	12	2 2	2	5	7	16*	4	1					40	4.85	3.31	4.15			
																		35	3.51
4	14	1 1	3	8	12*	8	2	2	6	13*	11	2	30	3.13	5.65	4.58			
																		40	3.28
4	15	1 2	3	1	5	2	6	7	13*	3	1		40	5.50	3.80	4.58			
																		30	3.80
Total				3	60	291	396	538*	235	166	70	45	16	11	1831	Grand mean: 3.96			

\* Mode

\*\* Mean num. of B's. per PMC in each anther

Chromosome counting was by far more difficult in the root-tips than in the PMC's, because the chromosomes were usually clustered. The only record obtained from Ta-wu 47 is given below:

Table 5. Numbers of B chromosomes scored in the root-tip cells of clone Ta-wu 47.

Num. of cells with resp. num. of B's				Total
1	2	3	4	
1	6	4	1	12

Again, there was an inter-cell variation in the number of B chromosomes. However, the range of variation was much limited as compared with that for PMC's. As recognizable from Table 5, the number of B chromosomes in root-tip cells ranged from one to four.

### Results of Variance Analysis

The results of variance analysis for clone Ta-wu 47, carried out according to a hierarchical classification (see Appendix), are shown in Table 6. The table shows that "between-anthers-within-spikelets" variance is highly significant, while all the others are not. This indicates that there are real differences between anthers.

Table 6. The results of variance analysis for the numerical variation of B chromosomes in the floral parts of clone Ta-wu 47.

Source of variation	DF	SS	MS	Expectation of MS	Test of hypothesis
Between panicles	2	10.301	5.151	$\sigma_e^2 + 36.493\sigma_a^2 + 68.353\sigma_s^2 + 128.833\sigma_b^2 + 596.177\sigma_p^2$	$F'_b = 0.059$ $DF_1 = 2, DF_2 = 17$
Between branches within panicles	15	1,168.706	77.914	$\sigma_e^2 + 36.588\sigma_a^2 + 59.904\sigma_s^2 + 95.914\sigma_b^2$	$F'_b = 1.594$ $DF_1 = 15, DF_2 = 12$
Between spikelets within branches	12	578.978	48.248	$\sigma_e^2 + 36.146\sigma_a^2 + 60.352\sigma_s^2$	$F'_s = 0.942$ $DF_1 = 12, DF_2 = 22$
Between anthers within spikelets	22	1,049.016	47.683	$\sigma_e^2 + 33.568\sigma_a^2$	$F'_a = 35.589^{**}$ $DF_1 = 22, DF_2 = 1,779$
Within anthers	1,779	2,383.547	1.340	$\sigma_e^2$	
Total	1,830	5,190.540			

\*\* Significant at 1% level.

### Discussion and Conclusion

The most striking fact featuring the B chromosomes found in the present material of *M. japonicus* is the occurrence of B's in varying numbers both

among the PMC's and among the root-tip cells from one and the same clone. Cases more or less similar to the present one have been reported by several workers. In the root-tips of some strains of *Zea mays* Darlington and Upcott (1941) reported that there was a certain degree of variation in the number of B chromosomes, which was considered to be due to a certain weakness in the centromere of the B's. Also in the root-tips of *Centaurea scabiosa* Fröst (1956) found that the standard B chromosomes showed a slight variation in number within the plant, and he believed that the numerical variation was caused by stickiness, which might sometimes prevent the separation of the daughter chromosomes. In four plants of *Poa alpina*, Müntzing (1948) found that the number of B chromosomes in the PMC's varied within the individual, not only in different years and in different panicles but also within the same anther loculus. However, he did not elaborate upon the explanation of this phenomenon. Bosemark (1957) found that in three plants of *Poa trivialis* there was a marked numerical variation of B chromosomes not only among flowers but also within flowers and individual anthers. He suggested that the variation might result from loss or non-disjunction of the B chromosomes at some stage of the early development of the panicles combined with similar events in pre-meiotic mitoses in the anthers. More recently Evans (1961) reported that in some individuals of *Helix pomatia*, sampled from two wild populations, the number of B chromosomes varied among primary spermatocytes within the individual. Such intra-individual variation, according to Evans, seemed to arise through (a) mitotic instability during the development of the organism thus resulting in the elimination of the B's from the somatic cells, or (b) somatic non-disjunction occurring either during the development of the organism as a whole or possibly only in the ovo-testes tissues.

As regards the present *Miscanthus* clones, the numerical variation of B chromosomes within the individual seems to be due to either (a) somatic elimination or (b) somatic non-disjunction, or both. In Wu-lai 13, the PMC's contain only one B chromosome or none (Table 3). Here the B-free PMC's may arise from somatic elimination of the B chromosome prior to meiosis, and so those containing one B chromosome may be regarded as the intact cells. The numerical variation of B chromosomes in the root-tips of Ta-wu 47 (Table 5) may also be attributed solely to somatic elimination, since non-disjunction of the B's was not found at the somatic anaphase. This will be taken up again later. The most amazing fact observed in the present investigation is the intra-individual variation of B-chromosome number in the floral parts of clones Wu-lai 1, Ta-wu 23 and Ta-wu 47, the B's being present in varying numbers in the PMC's within a clone (Tables 3 & 4) and even the mean numbers of B's of the three anthers in the same spikelet also differing from one another very significantly (Table 6). Presumably this is caused by the non-disjunction of B chromosomes at some stage prior to the advent of meiosis, as will be discussed in the following by using the data available from clone Ta-wu 47.

Assuming that chromosome elimination and cell selection do not occur, it

may be inferred for Ta-wu 47 that 38A+4B might be the original chromosome complement. This assumption is based on the following reasons:

(1) The mean number of B chromosomes per PMC in Ta-wu 47 was 3.96, which is very closely approximate to 4. In the absence of chromosome elimination and inter-cell competition, non-disjunction cannot change the mean number of B's for a given individual. If we had, for instance, an initial cell with 4 B chromosomes which would undergo non-disjunction at a certain rate, there would be after  $n$  cycles of cell division  $2n$  cells with varying numbers of B chromosomes. However, the mean number of B's per cell would be still 4 ( $=4 \cdot 2^n / 2^n$ ). In the case of Ta-wu 47, therefore, the mean 3.96 may be rounded up to represent its original number of B's, that is 4. Here the deviation  $d=4-3.96$  is not statistically significant ( $t=1.026$ ,  $P>30\%$ ). Therefore, it may be regarded as falling within the limits of sampling error.

(2) The modal number of B's in the pooled frequency distribution of B's in Ta-wu 47 was also 4. The mode will show the original number, so long as the B chromosomes undergoing non-disjunction are distributed to the daughter cells at random. This will be borne out later by a theoretical consideration on the sequence of non-disjunction.

(3) The largest number of B chromosomes found in root-tip cells was also 4. As non-disjunction was not found in the root-tip cells, the cell with the largest number of B's may be considered as retaining all the B chromosomes originally present in the embryo. The plausibility of this interpretation may be sustained by the two reasonings aforegiven.

If 38A+4B can be established as the original chromosome complement for clone Ta-wu 47, the variation from 0 to 10 in the PMC's would be accounted for by at least two cycles of somatic non-disjunction. The first cycle may take place at the stage of the formation of anther primordia, because the difference between anthers was highly significant and the anther mean did not as a rule exceed 8 (see Table 4, 17th column). During the early development of anthers, non-disjunction may also occur but only sporadically and at a low frequency. This can be evidenced by the occasional cases of bimodal and irregular distributions of B's as shown in Table 4. The second cycle of non-disjunction seems to take place immediately before the advent of meiosis, possibly involving the majority of archesporial cells. This view is supported by the wide range of numerical variation of B's among PMC's within the same anther (Table 4).

#### Theoretical Considerations on the Numerical Variation of B Chromosomes

Let us consider a group of initial cells with four B chromosomes. Denoting by  $p$  the probability that a B chromosome undergoes non-disjunction, and by  $q=1-p$  the probability of normal disjunction, and assuming that after non-disjunction the sister chromosomes are distributed into the daughter cells by chance, the frequencies of cells with various numbers of B chromosomes produced at the end of the first cycle of cell division are expected as follows:



Num. of B's per cell	Relative frequency
0, 8	$P_0 = \frac{1}{16} p^4$
1, 7	$P_1 = \frac{1}{2} p^3 q$
2, 6	$P_2 = \frac{1}{4} p^4 + \frac{3}{4} p^2 q^2$
3, 5	$P_3 = \frac{3}{2} p^3 q + 2 p q^3$
4	$P_4 = \frac{3}{8} p^4 + 3 p^2 q^2 + q^4$

This indicates that the first cycle of non-disjunction cannot give rise to cells with more than 8 B chromosomes (Cf. Table 4, 17th column). On the completion of the second cycle, however, we have

Num. of B's per cell	Relative frequency
0	$R_0$
1	$qR_1$
2	$\frac{1}{2} pR_1 + q^2 R_2$
3	$pqR_2 + q^3 R_3$
4	$\frac{1}{4} p^2 R_2 + \frac{3}{2} pq^2 R_3 + q^4 R_4$
5	$\frac{3}{4} p^2 q R_3 + 2 p q^3 R_4 + q^5 R_5$
6	$\frac{1}{8} p^3 R_3 + \frac{3}{2} p^2 q^2 R_4 + \frac{5}{2} p q^4 R_5 + q^6 R_6$
7	$\frac{1}{2} p^3 q R_4 + \frac{5}{2} p^2 q^3 R_5 + 3 p q^5 R_6 + q^7 R_7$
8	$\frac{1}{16} p^4 R_4 + \frac{5}{4} p^3 q^2 R_5 + \frac{15}{4} p^2 q^4 R_6 + \frac{7}{2} p q^6 R_7 + q^8 R_8$
9	$\frac{5}{16} p^4 q R_5 + \frac{5}{2} p^3 q^3 R_6 + \frac{21}{4} p^2 q^5 R_7 + 4 p q^7 R_8$
10	$\frac{1}{32} p^5 R_5 + \frac{15}{16} p^4 q^2 R_6 + \frac{35}{8} p^3 q^4 R_7 + 7 p^2 q^6 R_8$
11	$\frac{3}{16} p^5 q R_6 + \frac{35}{16} p^4 q^3 R_7 + 7 p^3 q^5 R_8$
12	$\frac{1}{64} p^6 R_6 + \frac{21}{32} p^5 q^2 R_7 + \frac{35}{8} p^4 q^4 R_8$
13	$\frac{7}{64} p^6 q R_7 + \frac{7}{4} p^5 q^3 R_8$
14	$\frac{1}{128} p^7 R_7 + \frac{7}{16} p^6 q^2 R_8$
15	$\frac{1}{16} p^7 q R_8$
16	$\frac{1}{256} p^8 R_8$

where

$$R_0 = (1 + \frac{1}{256}p^8)P_0 + (-\frac{1}{2}p + \frac{1}{128}p^7)P_1 + (-\frac{1}{4}p^2 + \frac{1}{64}p^6)P_2$$

$$+ (-\frac{1}{8}p^3 + \frac{1}{32}p^5)P_3 + \frac{1}{16}p^4P_4$$

$$R_1 = \frac{1}{16}p^7P_0 + (1 + \frac{7}{64}p^6)P_1 + (p + \frac{3}{16}p^5)P_2 + (-\frac{1}{4}p^2 + \frac{5}{16}p^4)P_3 + \frac{1}{2}p^3P_4$$

$$R_2 = \frac{1}{16}p^6P_0 + \frac{21}{32}p^5P_1 + (1 + \frac{15}{16}p^4)P_2 + (-\frac{3}{2}p + \frac{5}{4}p^3)P_3 + \frac{3}{2}p^2P_4$$

$$R_3 = \frac{7}{4}p^5P_0 + \frac{35}{16}p^4P_1 + \frac{5}{2}p^3P_2 + (1 + \frac{5}{2}p^2)P_3 + 2pP_4$$

$$R_4 = \frac{35}{8}p^4P_0 + \frac{35}{8}p^3P_1 + \frac{15}{4}p^2P_2 + \frac{5}{2}pP_3 + P_4$$

$$R_5 = 7p^3P_0 + \frac{21}{4}p^2P_1 + 3pP_2 + P_3$$

$$R_6 = 7p^2P_0 + \frac{7}{2}pP_1 + P_2$$

$$R_7 = 4pP_0 + P_1$$

$$R_8 = P_0$$

Now the range of variation has been widened, covering from 0 through 16 (Cf. Table 4, 5th-15th columns). By using Fisher's scoring method (cited by Mather, 1951; p. 86), the value of  $p$  was estimated to be 0.338. It was found,

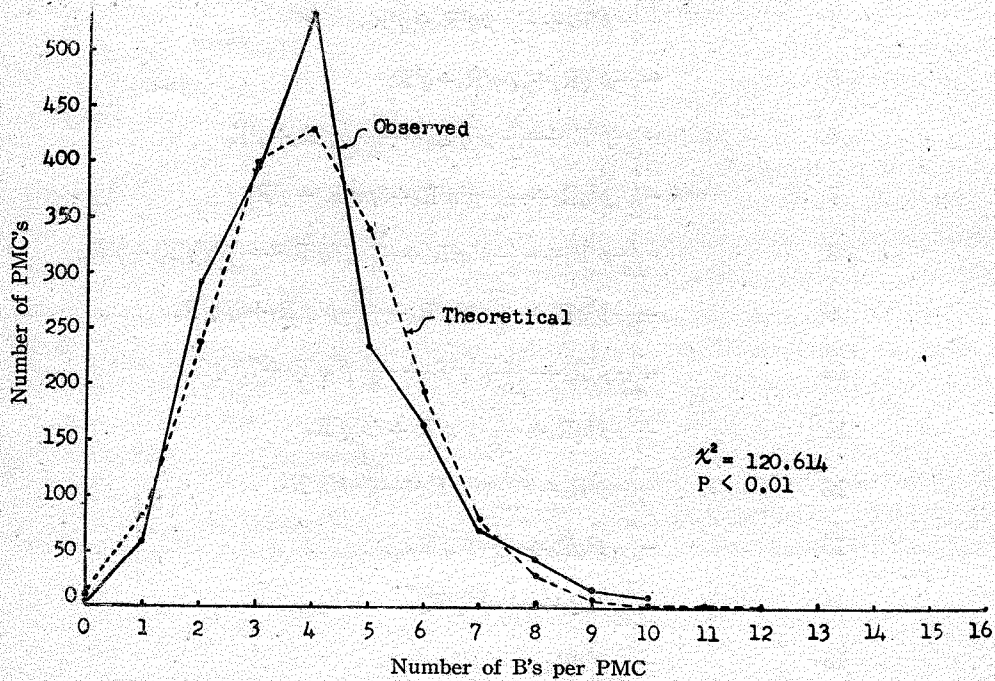


Fig. 12. Theoretical and observed frequency distributions of PMC's with various numbers of B chromosomes in clone Ta-wu 47.

as shown in Fig. 12, that the observed and the theoretical distributions appeared to be similar, though  $X^2$  test showed that the difference was significant. It may be due to a certain degree of somatic elimination of the B chromosomes, or differences in the mitotic rate among various cell types.

#### Summary

(1) Accessory or B chromosomes were found in four out of some 200 clones of *Miscanthus japonicus* Anderss. collected from various sites in Taiwan. The morphology and meiotic behavior of these B chromosomes were in general similar to those reported in other grass species by various workers.

(2) One of these clones, Wu-Lai 13, was found to have in the PMC's only one B chromosome or none. The PMC's without B chromosome might arise through somatic elimination prior to meiosis.

(3) The other three clones, namely, Wu-Lai 1, Ta-wu 23 and Ta-wu 47, were found to have varying numbers of B chromosomes in the PMC's, ranging from 0 to 10. Such an intra-individual variation was considered to be the outcome of somatic non-disjunction of the B chromosomes. In the root-tip cells of clone Ta-wu 47, however, the number of B chromosomes showed a variation ranging from 1 to 4. Somatic elimination was assumed to account for such a variation, insofar as not a single instance of non-disjunction was found in the dividing root-tip cells.

(4) For clone Ta-wu 47, the original number of B chromosomes was assumed to be four. Variance analysis of the numerical variation of B chromosomes was made in accordance with a hierarchical classification. The results suggested that there might be two major cycles of somatic non-disjunction, one responsible for the significant differences between anthers of the same spikelet and the other for the variation among PMC's of the same anther. The numerical variation caused by non-disjunctional cycles were theoretically investigated. The probability that a B chromosome undergoes somatic nondisjunction was estimated to be 0.338.

Appendix.

Model of variance analysis for a hierarchical classification with four ranks of unequal numbers.

Source of variation	DF	SS	MS	Expectation of MS
Between panicles	$\alpha - 1$	$SSP = \sum \frac{Y_i^2 \dots}{N_{i\dots}} - \frac{Y^2 \dots}{N \dots}$	$\frac{SSP}{\alpha - 1}$	$\sigma^2_e + c_1\sigma^2_a + c_2\sigma^2_s + c_3\sigma^2_b + c_4\sigma^2_p$
Between branches within panicles	$R - \alpha$	$SSB = \sum \sum \frac{Y^2_{ij\dots}}{N_{ij\dots}} - \sum \frac{Y^2_{i\dots}}{N_{i\dots}}$	$\frac{SSB}{R - \alpha}$	$\sigma^2_e + c_5\sigma^2_a + c_6\sigma^2_s + c_7\sigma^2_b$
Between spikelets within branches	$Q - R$	$SSS = \sum \sum \sum \frac{Y^2_{ijk\dots}}{N_{ijk\dots}} - \sum \sum \frac{Y^2_{ij\dots}}{N_{ij\dots}}$	$\frac{SSS}{Q - R}$	$\sigma^2_e + c_8\sigma^2_a + c_9\sigma^2_s$
Between anthers within spikelets	$P - Q$	$SSA = \sum \sum \sum \frac{Y^2_{ijkl\dots}}{N_{ijkl\dots}} - \sum \sum \frac{Y^2_{ijk\dots}}{N_{ijk\dots}}$	$\frac{SSA}{P - Q}$	$\sigma^2_e + c_{10}\sigma^2_a$
Within anthers	$N \dots - P$	$SSE = \sum \sum \sum \sum y^2_{ijklm} - \sum \sum \sum \frac{Y^2_{ijkl\dots}}{N_{ijkl\dots}}$	$\frac{SSE}{N \dots - P}$	$\sigma^2_e$
Total	$N \dots - 1$	$SST = \sum \sum \sum \sum y^2_{ijklm} - \frac{Y^2 \dots}{N \dots}$	$\frac{SST}{N \dots - 1}$	

Notes:  $y_{ijklm}$  = number of B chromosomes in the  $m$ th PMC of the  $l$ th anther of the  $k$ th spikelet of the  $j$ th branch of the  $i$ th panicle.

$n_{ijkl}$  = num. of PMC's in the  $l$ th anther of the  $k$ th spikelet of the  $j$ th branch of the  $i$ th panicle.

$\delta_{ijk}$  = num. of anthers in the  $k$ th spikelet of the  $j$ th branch of the  $i$ th panicle.

$\gamma_{ij}$  = num. of spikelets on the  $j$ th branch of the  $i$ th panicle.

$\beta_i$  = num. of branches in the  $i$ th panicle.

$\alpha$  = num. of panicles from one and the same plant.

$$N_{ijk\dots} = \sum_{l=1}^{\delta_{ijk}} n_{ijkl\dots} \quad N_{ij\dots} = \sum_{k=1}^{\gamma_{ij}} N_{ijk\dots} \quad N_{i\dots} = \sum_{j=1}^{\beta_i} N_{ij\dots} \quad N \dots = \sum_{i=1}^{\alpha} N_{i\dots}$$

$$Y_{ijkl\dots} = \sum_{m=1}^{n_{ijkl\dots}} y_{ijklm} \quad Y_{ijk\dots} = \sum_{l=1}^{\delta_{ijk}} Y_{ijkl\dots} \quad Y_{ij\dots} = \sum_{k=1}^{\gamma_{ij}} Y_{ijk\dots} \quad Y_{i\dots} = \sum_{j=1}^{\beta_i} Y_{ij\dots} \quad Y \dots = \sum_{i=1}^{\alpha} Y_{i\dots}$$

$$P = \sum \sum \sum \delta_{ijk} \quad Q = \sum \sum \gamma_{ij} \quad R = \sum \beta_i$$

$$c_1 = \frac{1}{\alpha - 1} \left\{ \sum_i \left( \frac{\sum \sum \sum n^2_{ijkl\dots}}{N_{i\dots}} \right) - \frac{\sum \sum \sum n^2_{ijkl\dots}}{N \dots} \right\} \quad c_2 = \frac{1}{\alpha - 1} \left\{ \sum_i \left( \frac{\sum \sum N^2_{ijk\dots}}{N_{i\dots}} \right) - \frac{\sum \sum N^2_{ijk\dots}}{N \dots} \right\}$$

$$c_3 = \frac{1}{\alpha - 1} \left\{ \sum_i \left( \frac{\sum_j N^2_{ij\dots}}{N_{i\dots}} \right) - \frac{\sum_j N^2_{ij\dots}}{N \dots} \right\} \quad c_4 = \frac{1}{\alpha - 1} \left( N \dots - \frac{\sum_i N^2_{i\dots}}{N \dots} \right)$$

$$c_5 = \frac{1}{R - \alpha} \left\{ \sum \sum \left( \frac{\sum_k n^2_{ijk\dots}}{N_{ij\dots}} \right) - \sum_i \left( \frac{\sum \sum n^2_{ijk\dots}}{N_{i\dots}} \right) \right\} \quad c_6 = \frac{1}{R - \alpha} \left\{ \sum \sum \left( \frac{\sum_k N^2_{ijk\dots}}{N_{ij\dots}} \right) - \sum_i \left( \frac{\sum \sum N^2_{ijk\dots}}{N_{i\dots}} \right) \right\}$$

$$c_7 = \frac{1}{R - \alpha} \left\{ N \dots - \sum_i \left( \frac{\sum_j N^2_{ij\dots}}{N_{i\dots}} \right) \right\} \quad c_8 = \frac{1}{Q - R} \left\{ \sum \sum \sum \left( \frac{\sum_l n^2_{ijkl\dots}}{N_{ijk\dots}} \right) - \sum \sum \left( \frac{\sum \sum n^2_{ijkl\dots}}{N_{ij\dots}} \right) \right\}$$

$$c_9 = \frac{1}{Q - R} \left\{ N \dots - \sum \sum \left( \frac{\sum_k N^2_{ijk\dots}}{N_{ij\dots}} \right) \right\} \quad c_{10} = \frac{1}{P - Q} \left\{ N \dots - \sum \sum \sum \left( \frac{\sum_l n^2_{ijkl\dots}}{N_{ijkl\dots}} \right) \right\}$$

$\sigma^2_e$  is the variance of random error, while  $\sigma^2_a, \sigma^2_s, \sigma^2_b$  and  $\sigma^2_p$  are variances between anthers, spikelets, branches and panicles, respectively.

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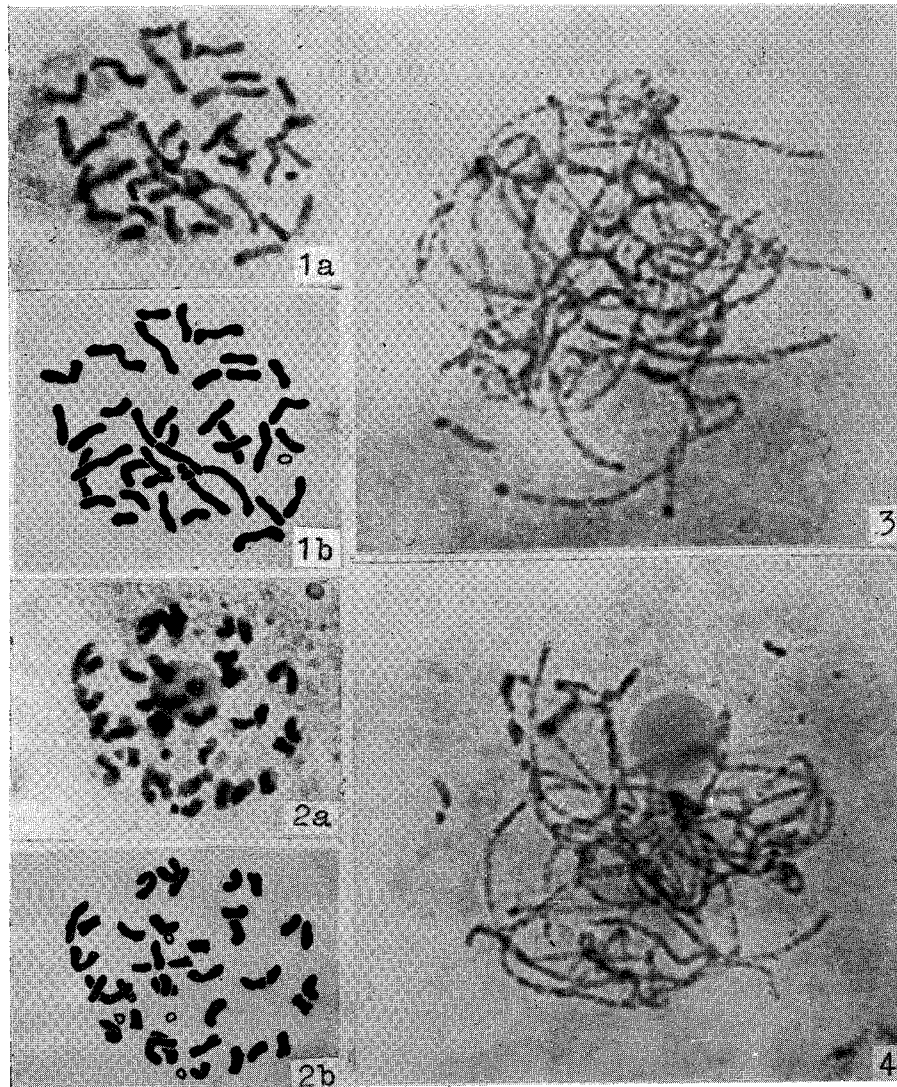
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## *Miscanthus japonicus* Anderss. 的額外染色體數 之體內變異

(中文摘要)

翁 登 山

1. 從臺灣各地採集的二百株 *Miscanthus japonicus* 中，有四株具有額外染色體，其減數分裂行為和形態與前人在其他禾本科植物中所發現者大致相同。
2. 上述四株中，有一株「烏來 13 號」在花粉母細胞中有時含有一個額外染色體，有時完全不含額外染色體。後者可能是在減數分裂前額外染色體從體細胞中消失 (Somatic elimination) 所致。
3. 其餘烏來 1 號，大武 23 號及大武 47 號等三株，每株在花粉母細胞中均含有 0 ~ 10 個額外染色體。這種額外染色體數之體內變異現象可能起因於體細胞分裂時所發生的染色體不分離 (Somatic non-disjunction)。又大武 47 號的根尖細胞亦含有 1~4 個額外染色體，其數目變動的原因似乎也是 Somatic elimination，因根尖細胞中並未發現染色體不分離的跡象。
4. 大武 47 號的原有額外染色體數似應為 4。根據單向逐級分類法 (Hierarchical classification) 作變方分析的結果，顯示額外染色體數的體內變異似因體細胞在減數分裂前曾經發生兩次染色體不分離使然。其中一次可能發生在原始花芽分化時期，另一次似乎發生在孢原細胞分裂時期。依筆者的推算，一個額外染色體可能發生不分離現象之平均機率約為 0.338。



- Fig. 1. Somatic plate from clone Ta-wu 47,  $2n=38A+1B$ .  
 Fig. 2. Somatic plate from Ta-wu 47,  $2n=38A+4B$ .  
 Fig. 3. One B (7 o'clock) with subterminal centromere at pachynema in Ta-wu 47.  
 Fig. 4. Two B's at pachynema in Ta-wu 47; one has subterminal centromere (9 o'clock), the other median centromere (1 o'clock).

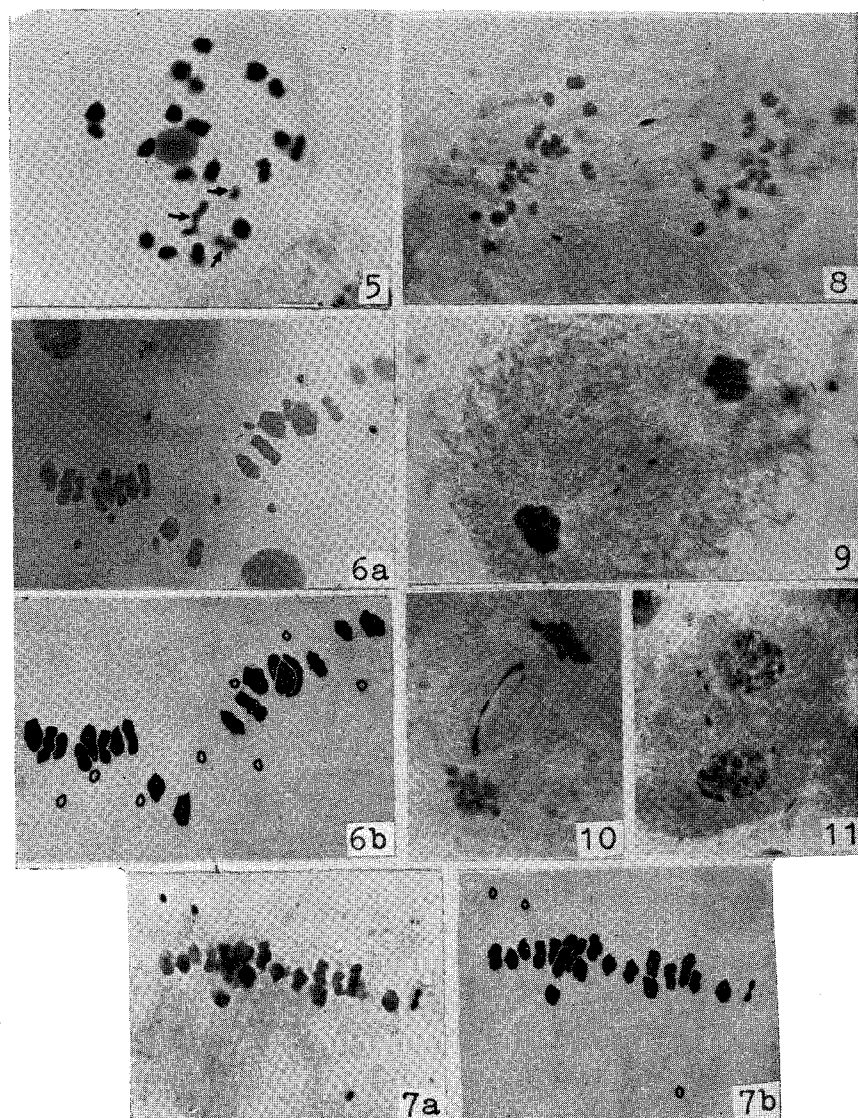


Fig. 5. Diakinesis in clone Ta-wu 23,  $19A_{II}+1B_{IV}+1B_{III}+1B_I$  (the B's are indicated with arrows).

Fig. 6. First metaphase in Ta-wu 47,  $19A_{II}+8B_I$ .

Fig. 7. 1st metaphase in Ta-wu 23,  $19A_{II}+1B_{II}+3B_I$ .

Fig. 8. 1st anaphase in Ta-wu 47 showing one laggard.

Fig. 9. 1st anaphase in Ta-wu 47, 4 laggards.

Fig. 10. 1st anaphase in Ta-wu 47 showing a chromatid bridge.

Fig. 11. Interphase in Ta-wu 47 showing 4 micronuclei.