CYTOLOGICAL STUDIES ON TAIWAN GRASSES
I. TRIBE PANICEAE[1]

CHI-CHANG CHEN AND CHIEN-CHANG HSU[2]

Of about 250 species of grasses found in Taiwan, few cytological studies have been carried out so far. This paper is a part of our cytological investigations of Taiwan grasses. In addition to chromosome numbers, meiotic behavior of chromosomes was also studied. It is familiar to the authors that the study of meiotic behavior of chromosomes will give better understanding to some questionable species.

The Paniceae is the largest tribe of grasses found in Taiwan. According to Hsu (1961), 69 species and 19 varieties, belonging to 21 genera, are recognized. In the present study, all specimens were identified by the junior author. The arrangement of genera in tribe follows Reeder's system (1948). References to previous record of chromosome numbers which are not available to the authors or published in a language not familiar to them may be found in Darlington and Wylie (1955), Myers (1947) and Cave (1958, 1959, 1960).

Materials and Methods

The chromosome studies were made on pollen mother cells. All materials were collected from fields. Buds were fixed in the standard 3:1 alcohol-glacial acetic solution, and the anthers were smeared and stained with either acetocarmine or propino-carmine. All observations were made at the magnification of 900x and all drawings were made with a camera lucida. The bud collections sometimes were made from several plants of a population and the chromosome count as reported here may represent counts from one to several individual plants from the same population. Complete sets of herbarium specimens were prepared and deposited in the Herbarium of National Taiwan University. Most chromosome counts reported here are indicated by gametic number. The chromosome configurations at diakinesis or metaphase I were also reported when meiotic behavior was irregular, but only the major case was listed in the table. The theoretical

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(2) Assistant Research Fellow of the Institute of Botany, Academia Sinica and Assistant of the Department of Botany, National Taiwan University respectively.

basic chromosome number for a species or taxon is referred to as "x".

Results and Discussions

Panicum L.

Previous reports (Brown, 1948, 1950, 1951; Burton, 1942; Church, 1929; Darlington and Wylie, 1955; de Wet, 1954, 1960; de Wet and Anderson, 1956; Gould, 1958; Tateoka, 1954, 1955, 1956; Warmke, 1951) show that most species of *Panicum* have a basic number of $\times=9$ though in some species the basic numbers of 8 to 11 have also been reported. In the present study, counts were obtained for eight species which were either native or cultivated in Taiwan. *P. incomtum*, *P. brevifolium*, *P. cordatum*, *P. psilopodium* and *P. bisulcatum* were found to be tetraploid with 9 as the basic number. Meiosis of these species were normal except *P. bisulcatum* (Fig. 1), *P. bisulcatum* and *P. psilopodium* which were previously reported to be hexaploid with 9 as the basic number (de Wet, 1954; Tateoka, 1954; Ramanathan, 1950).

Cytology of five varieties of *P. maximum* was first reported by Warmke (1951) as having 32 and 48 somatic chromosomes. Having studied meiosis of microsporocytes he concluded that all the 32-chromosome varieties were autotetraploid (forming association of four), and the 48-chromosome variety was autohexaploid (forming association of six). In a later study, de Wet (1954) demonstrated that 9 was the basic number of this species. He studied one taxon from South Africa with $2n=18$. In this study, one taxon collected from Nantow County was found to have 32 chromosomes with various combinations of univalent, bivalent and quadrivalent associations at diakinesis. This supports Warmke's data that eight is the basic number of this species. Since no recognizable cases of eight quadrivalents and eight hexavalents have been found in cells of the 32-chromosome varieties and 48-chromosome variety, it seems to the authors that terms of segmental allotetraploid and segmental allohexaploid are more suitable to both cases.

Counts of $n=27$ were obtained for two taxa of *P. paludosum*. This species was the only hexaploid *Panicum* reported in this paper.

Cytology of *P. repens* was first reported by Krishnaswamy (1940) as having forty chromosomes. Later on, one tetraploid from South Africa and one pentaploid from Japan both based on $x=9$ were obtained by de Wet (1956) and Tateoka (1956). No report of the meiotic behavior was given. In the present study, the count of $2n=45$ for this species was in agreement with that of Tateoka. At metaphase I, there were 27 elements 18II+9I (Fig. 10), and other configurations such as 17II+11I and 19II+7I were occasionally found (Fig. 11, 12). Laggards at anaphase I and anaphase II (Fig. 13, 14) revealed that other stages were also irregular. Spikelets of many plants were examined but no seed setting has ever been found. These data led the authors to believe that the so-called *P. repens* found in Taiwan and that studied by Tateoka (1956) might be a hybrid and it is propagated by vegetative means.

Brachiaria (Trin.) Griseb.

Four species are found in Taiwan. The count of *B. reptans* agreed with those of Brown (1950, as *Panicum reptans*) and Sharma and Jhuri (1959). The count of n=18 for *B. villosa* was the first cytological record. *B. reptans* and *B. villosa* are similar in gross morphology, but they are easy to be distinguished cytologically, since the basic numbers of these two species are different. The count of n=36 was obtained for *B. distachya.* However, 2n=36 for this species has also been reported (Krishnaswamy, 1940).

Ichnanthus Beauv.

Previous cytological record for this genus has not been found. The count of n=20 for *I. vicinus* reveals that as *Paspalum* and *Isachne,* the basic number of *Ichnanthus* may be x=10.

Echinochloa Beauv.

Counts of n=27 were obtained for *E. colonum, E. crusgalli* and *E. crusgalli* var. *caudata.* The count of *E. colonum* was in agreement with that of de Wet (1954), but 2n=36 (Brown, 1950) and 2n=48 (Krishnaswamy, 1949) for this species have also been reported. Several kinds of chromosome numbers, 2n=36 (Brown, 1948), n=21 (Church, 1929), 2n=48 (Rau, 1929) and 2n=54 (Tateoka, 1954) have been reported for *E. crusgalli,* but only that reported by Tateoka was confirmed by the present study. Inspite of the divergent records, the present study shows that the basic number of *Echinochloa* is x=9. Similar basic number has been suggested by Brown (1948).

Oplismenus Beauv.

Of about 3 species and 6 varieties found in Taiwan, only 2 varieties were studied cytologically. Counts of n=36 were obtained for both *O. compositus* var. *intermedius* and *O. compositus* var. *Owatarii.*

Sacciolepis Nash

The two species, *S. angusta* and *S. indica* were found in Taiwan, but only the latter was studied cytologically. Counts of n=9 were obtained for two taxa of *S. indica.*

Cyrtococcum Stapf

The count of n=18 was obtained for *C. patens.* Chromosomes of this species were found to be small in size and with 9 as the basic number.

Digitaria Heist, ex Haller

Digitaria is distributed in the warmer parts of the Old World. About 11 species and 2 varieties are found in Taiwan. Three kinds of basic number, x=9, x=15 and x=17 have been listed for this genus (Darlington and Wylie 1955). In the present study, chromosome numbers were found to be in a polyploid series of x=9. Counts of n=9 were obtained for *D. chinensis*, *D. chinensis* var. *hirsuta* and *D. longiflora;* n=18 for *D. Henryi*, *D. leptalea* var. *reticulmis*, *D. magna*, *D. Shimadama* and *D. violascens;* n=27 for *D. sericea;* n=36 for *D. microbachne;* and both n=27 and 2n=27 for *D. adscendens*.

The genus *Digitaria* presents many taxonomical difficulties. Cytological difference between *D. adscendens* and *D. chinensis* has been pointed out by Ono and Tateoka (1953) that *D. adscendens* had about 54 somatic chromosomes while the chromosome number of *D. chinensis* was 2n=18. Counts for two taxa of *D. chinensis* were in agreement with that of Ono and Tateoka. However, two kinds of chromosome number, n=27 and 2n=27 were obtained for *D. adscendens*. Morphologically, the taxon of *D. adscendens* with 27 chromosomes differs from the taxon with 54 chromosomes in nerves of the sterile lemma and length of the pedicel of spikelets. Meiosis in microsporocytes of the latter was found to be normal while the former very irregular. In the taxon with 27 chromosomes, 8 or 9 univalents were usually found at diakinesis and metaphase I in all microsporocytes (Fig. 29-31). As a result, lagging chromosomes at anaphase I were found with the same number as univalents at diakinesis and metaphase I (Fig. 32). At metaphase II, excluded chromosomes were observed (Fig. 33). Possibly, the taxon with 27 chromosomes and irregular meiotic division is a hybrid, but morphologically it resembles to *D. adscendens*.

Two taxa of *D. violascens* were obtained and studied. One taxon has stiff hairs at sheaths and grows in high mountains, while the other has a wide distribution and without stiff hairs. There was no difference in chromosome number between these two taxa, except 4 nucleolar-like droplets which were found at diakinesis in the hispid taxon (Fig. 45).

Eriochloa H. B. K.

The count of n=18 was obtained for *E. procera* and meiotic behavior was found to be regular. Similar chromosome number has been reported by Ramen *et al* (1959). Previous reports (Brown, 1950, 1951; de Wet, 1960) show that chromosome numbers of *Eriochloa* are in multiples of 9, and this was confirmed by the present study.

Paspalum L.

Counts of n=20 were obtained for *P. conjugatum* and *P. longifolium*. These two species took a peculiar way of meiosis which was very similar to that of *Paspalum secans* (Snyder 1957). Possibly synapsis did not take place at the zygotene stage. As a result of this, 40 chromosomes were observed to be completely unpaired at diakinesis and metaphase I. The stage of prometaphase I was comparatively prolonged, but finally all chromosomes (univalents) were capable of going to the equatorial plate where they clumped together. It was uncertain whether chromosomes were paired together at late metaphase I when they clumped together at the equatorial plate, but in some cells observed they could separate normally without laggards. However, thorough cytological and taxonomic studies would be necessary before a detailed result can be got.

Two kinds of chromosome number, 2n=50 (Krishnaswamy, 1940; Tateoka, 1955) and 2n=40 (Brown, 1948; Smith, 1948; de Wet and Anderson, 1956) have been reported for *P. dilatatum.* From available data it was found that taxa with 2n=40 do occur in America, Australia and Africa while taxa with 2n=50 are found in Asia. Meiosis of the 40-chromosome taxa has been reported to have 30 elements 10II+10I+10I or 20 normal bivalents at diakinesis and metaphase I (Smith, 1955), but only somatic cells have been studied for the 50-chromosome taxa. Tateoka (1955) studied one taxon of Japan with 2n=50 and suggested that the basic number is five in the Paniceae. In this study, meiosis of microsporocytes of one taxon which is widely distributed over this island was studied with 20 bivalents and 10 univalents at metaphases I (Fig. 48). Laggards were common at anaphase I and telophase I, and the maximum number was 10 (Fig. 50).

Taxonomic and cytological differences between *P. distichum* and *P. vaginatum* have been pointed out by Brown (1948) that *P. vaginatum* which was a diploid species with 2n=20 chromosomes was found along seacoasts in wet, often brackish sand while *P. distichum* which was a tetraploid species with 2n=40 chromosomes was not found in brackish water. The present study of these two species was in agreement with Brown's observation. However, another kind of chromosome number, 2n=60 as reported by Parodi (1946) was obtained for one taxon of *P. distichum.* Meiotic behavior of microsporocytes of the taxon with 40 chromosomes was found to be regular with 20 bivalents at diakinesis (Fig. 51) while meiosis of the taxon with 60 chromosomes was abnormal. Univalents could be observed in microsporocytes in a range from 0 to 12 (Fig. 52, 53). Quadrivalents were occasionally found and the number was not more than 2. Either divided or undivided laggards were found at anaphase I and the maximum number was 20 (Fig. 54). Micronuclei were found at tetrad stage in a range from 2 to 16. The above data show that at least 10 pairs of chromosomes are not entirely paired. This may be due to either hybrid origin of the taxon or gene-controlled desynapsis.

The count of n=20 for *P. scrobiculatum* was in agreement with that of Avdulov (1928).

Setaria Beauv.

Counts of n=36 for *S. geniculata,* n=27 for *S. palmifolia* and n=9 for *S. viridis* var. *pachystachys* were in agreement with those of Brown (1948), Krishnaswamy *et al.* (1954) and Tateoka (1954) respectively.

All species of *Setaria* so far reported have chromosomes in multiples of 9. The exceptional one, *S. chondranchne,* reported by Ono and Tateoka (1953) has 38 somatic chromosomes. It is known to the authors that if

Ono and Tateoka's count is not in error, the plant which they studied might be an aneuploid.

Pseudoraphis Griff.

The genus *Pseudoraphis* has not been studied cytologically. In the present study, a complete convincing count was not obtained because of the indistinct staining, the stickiness of the chromosomes and the lack of sufficient materials. However, the count of n=ca. 20 for *P. squarrosa* suggests that the basic chromosome number of *Pseudoraphis* may be x=10. Meiotic behavior of chromosomes was found to be very irregular. Other than bivalents, all of the cells had univalents at metaphase I and the numbers were usually more than ten. Excluded chromosomes and fragments were also found at metaphase II (Fig. 63). *Pennisetum* Rich.

Only one species, *P. alopecuroides*, is found in Taiwan. The count of n=9 for this species was in agreement with that of Ono and Tateoka (1953).

Two basic chromosome numbers, 7 and 9, have so far been reported for members of the genus *Pennisetum*. However, Swaminathan and Nath (1956) reported the somatic chromosome numbers 10 and 32 in the species *P. ramosum* and *P. massaicum* and suggested two additional basic numbers, 5 and 8 for this genus. They further proposed that 5 is the original basic number in this genus and that 7, 8 and 9 have been derived from it.

Cenchrus L.

Cytology of *Cenchrus* has been studied by several authors (Brown, 1948, 1950; de wet and Anderson, 1956; Tateoka, 1955; Gould, 1958). Previously reported data reveal that basic numbers of this genus are various. The two common basic numbers which occurred in this genus are x=9 and x=17. The authors agree with Brown (1948) that the species with x=17 might originate from the tetraploid species of x=9 by reducing the chromosome numbers. In the present study, the count for *Cenchrus calycubatus* was n=34 with normal bivalents at metaphase I. Chromosomes were found to be large for the Paniceae.

Isachne R. Br.

Isachne is a genus of about 80 species found in tropical and temperate regions. Only one species, *I. globosa* has been studied cytologically by Tateoka (1954).

Counts of n=20 and n=30 were obtained for *I. nipponensis* and *I. albens* respectively. Meiotic behavior of these two species was regular.

The count of n=30 for one taxon of *I. globosa* was in agreement with that of Tateoka (1954). But the count for another taxon showed that it had ca. 90 chromosomes and the meiotic behavior was found to be very irregular. Many univalents were observed at diakinesis and metaphase I. The number of univalents at diakinesis could not be determined since in some cases it was uncertain whether two chromosomes were paired together forming bivalent or they were just lain together at random (Fig. 68). However, from the number of laggards at anaphase I (Fig. 70, 71) it was known that univalents at diakinesis were more than 20. Laggards were either divided (Fig. 71) or undivided (Fig. 70). Morphologically, the taxon with ca. 90 chromosomes differs from the taxon with 60 chromosomes (n=30) in hairy leaves. Since the latter is considered to be the typical *I. globosa*, the taxon with ca. 90 chromosomes and pubescent leaves might be a hybrid.

Three nucleolar-like droplets were observed at diakinesis in both taxa of *I. globosa* (Fig. 67, 68). The presence of droplets of staining material may be due to an over-production of nucleolar substances. It seems logical to infer that the presence of the same number of droplets in both taxa has some phylogenetical significance since Brown and Emery (1957) has found that the character of persistent nucleoli is apparently systematic value to grasses.

Thuarea Pers.

Previous cytological record for this genus has not been found. The present study of *T. involuta* showed that all cells had 9 bivalents at diakinesis and other stages were found to be normal. The basic chromosome number of the *Thuarea* is x=9.

Summary

1. Chromosome numbers and chromosome behavior of 41 species and 6 varieties of the tribe Paniceae, belonging to 16 genera, are reported in this paper. Cytology of the genera *Cyrtococcum*, *Ichnanthus*, *Pseudoraphis* and *Thuarea* are reported for the first time.

2. The basic chromosome numbers of the genera of the Paniceae are discussed. The author is of the opinion, that 10 or 5 may be the original basic number of the Paniceae from which all other basic numbers, 7, 8, 9, 17 have derived.

3. The peculiar way of meiotic division in microsporocytes of *Paspalum conjugatum* and *Paspalum longifolium* are reported. A thorough cytological study of these species may illuminate many problems of meiosis, especially of synapsis.

4. Irregular meiotic divisions are found in several taxa. From the meiotic behavior of the species of *Digitaria adscendens*, *Panicum repens* and *Paspalum dilatatum*, it is evident that hybridization is a common process in the evolution and speciation of grasses.

5. Nucleolar-like droplets are found at diakinesis in three taxa of the tribe Paniceae. Their presence may be due to an over-production of nucleolar substances and the systematic value of these droplets is also suggested.

臺灣禾本科植物細胞學的研究 一、黍族

陳 其 昌 許 建 昌

本報告包括禾本科植物黍族中41種及 6 變種染色體數目及減數分裂時染色體行爲的研究；其中 21 種及 6 變種過去未曾報告過。作者等研究時發現 *Paspalum conjugatum* 及 *P. longifolium* 之減數分裂甚爲奇特：染色體在肥厚期及第一中期均呈不配對現象。至於減數分裂時其他諸期染色體的變化，以後再作詳細的報告。染色體之不正常現象，曾在數種植物中發現，如 *Panicum repens, Digitaria adscendens, Paspalum dilatatum, Paspalum distichum, Isachne globosa, Pseudoraphis squarrosa* 等，此說明雜種作用在禾本科植物中非常普遍。(摘要)

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Table 1. Chromosome numbers in Taiwan grasses

Species	Number	n	Fig.	Authority (2n)
Panicum × =8, 9				
bisulcatum Thunb.	HC-937	18	1	36 Avdulov 1931
				54 de Wet 1954
brevifolium L.	HC-1333	18	2	
cordatum Buse	C-51	18	3	
incomtum Trin.	HC-1332	18	4	
maximum Jacq.	HC-1389	16	5,6	32,48 Warmke 1951
				18 de Wet 1954
paludosum Roxb.	C-78	27	7	
paludosum Roxb.	K-3561	27	8	
psilopodium Trin.	HC-602	18	9	54 Ramanathan 1950
repens L.	C-1	18II+9I	10-15	40 Krishnaswamy 1940
				36 de Wet & Anderson 1956
				45 Tateoka 1956
Brachiaria × =7, 9				
distachya (L.) A. Camus	C-72	36	16	36 Krishnaswamy 1940
reptans (L.) A. Camus	C-79	7	17	14 Brown 1950
				14 Sharma & Jhuri 1959
villosa A. Camus	C-109	18	18	
Ichnanthus × =10				
vicinus (F.M. Bail.) Merr.	HC-904	20	19	
Echinochloa × =9				
colonum (L.) Beauv.	HC-829	27	20	36 Brown 1948
				48 Krishnaswamy & H. 1949
				54 de Wet 1954
crusgalli (L.) Beauv.	HC-982	27	21	48 Rau 1929
				42 Church 1929
				36 Brown 1948
				54 Tateoka 1954
crusgalli (L.) Beauv. var. *caudata* Kitagawa	K-3562	27	22	
Oplismenus × =9				
compositus (L.) Beauv. var. *intermedius* Ohwi	HC-908	36	23	
compositus (L.) Beauv. var. *intermedius* Ohwi	HC-924	36		
compositus (L.) Beauv. var. *intermedius* Ohwi	C-36	36		
compositus (L.) Beauv. var. *Owatarii* Ohwi	C-106	36	24	
Sacciolepis × =9				
indica (L.) Chase	C-46	9	25	
indica (L.) Chase	C-114	9	26	
Cyrtococcum × =9				
patens (L.) A. Camus	HC-1339	18	27	
Digitaria × =9				
adscendens (H.B.K.) Henr.	C-132	27	28	54 Ono & Tateoka 1953
adscendens (H.B.K.) Henr.	C-124	9II+9I	29-33	36 Nath & Swaminathan 1957
chinensis Horn.	C-31	9	34	18 Ono & Tateoka 1953
chinensis Horn.	C-37	9		
chinensis Horn. var. *hirsuta* Ohwi	HC-1250	9	35	
Henryi Rendle	C-30	18	36	
Henryi Rendle	C-32	18		
Henryi Rendle	C-83	18		
leptalea Ohwi var. *reticulmis* Ohwi	HC-1230	18	37	
longiflora (Retz.) Pers.	H-471	9	38	18 de Wet & Anderson 1956
magna (Honda) Tuyama	C-96	18	39	
microbachne (Presl) Henr.	HC-1130	36	40	
sericea Honda	C-53	27	41	
Shimadama Ohwi	C-97	18	42-44	
violascens Link.	C-39	18	45	
violascens Link.	C-54	18		
Eriochloa × =9				
procera (Retz.) C.E. Hubb.	C-74	18	46	36 Raman *et al* 1959

Table 1. (Continued)

Species	Number	n	Fig.	Authority (2n)
Paspalum × =10				
conjugatum Berg.	C-28	20 (asynaptic)	47	
dilatatum Poir.	C-8	20II+10I	48-50	50 Krishnaswamy 1940 40 Brown 1948 40 Smith 1948 50 Tateoka 1955 40 de Wet & Anderson 1956
distichum L.	C-135	20	51	48 Burton 1942
disticnum L.	C-134	30	52-54	60 Parodi 1946 40 Brown 1948
longifolium L.	HC-1064	20 (asynaptic)	55,56	
scrobiculatum L.	C-25	20	57	40 Avdulov 1928
vaginatum Swartz	C-21	10	58	20 Brown 1948
Setaria × =9				
geniculata (Lam.) Beauv.	C-129	36	59	72 Brown 1948
genicnlata (Lam.) Beauv.	C-60	36		
palmifolia (Koening) Stapf.	C-13	27	60	54 Krishnaswamy 1954
viridis (L.) Beauv. var. *pachystachys* Makino	C-20	9	61	
Pseudoraphis × =10				
squarrosa (L.f.) Chase	HC-614	ca. 20	62,63	
Pennisetum × =9				
alopecuroides (L.) Spreng.	HC-936	9	64	18 Ono d Tateoka 1953
Cenchrus × =17				
calyculatus Cavan.	C-82	34	65	
Isachne × =10				
albens Trin	C-44	30	66	
globosa (Thunb.) O. Kuntze	C-103	30	67	60 Tateoka 1954
globosa (Thunb.) O. Kuntze	C-130	2n=ca. 90	68-71	
nipponensis Ohwi	C-14	20	72	
Thuarea × =9				
involuta R. Br.	HC-1025	9	73	