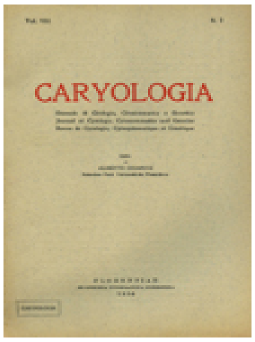

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(With 29 figures)

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CYTOLOGY OF SOME OF THE MILLETS

by

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(With 29 figures)

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CONTENTS

Introduction

Millets comprise a heterogenous assemblage of cereals, all being members of the family Gramineae. Their importance cannot be overemphasized in view of their large scale usage as the next to staple food in most of the countries. Several of the genera, which comprise the millets of the Indian subcontinent, include mainly the *Eleusine,* the *Setaria,* the *Pennisetum,* the *Sorghum,* the *Hordeum* and the *Triticum.* Not only most of these are cultivated in different agricultural stations, but at the same time a number of allied species are also found as wilds in nature.

Immense breeding work has been successfully carried out on practically all the members in India. The result has been the production of a number of improved strains and varieties, which have become of high commercial and economic value. Needless to mention that even some of these members have been crossed successfully with other genera (vide

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HECTOR, 1936). These are the reasons why millets are often cited as best illustrations of the importance of plant breeding work in plant improvement.

In spite of the accumulation of such a tremendous amount of data on the genetics of these members, our knowledge as to their cytology, excepting of *Sorghum* and *Triticum,* done at different centres is quite nebulous. No doubt researches are not absolutely lacking on this aspect and certain amount of results is at present on record, but these are no doubt meagre and just sufficient for undertaking any breeding project. Practically speaking, critical work involving detailed karyotypes of all their members have not yet been attempted.

Importance of karyotype analysis along with the meiotic behaviour is being more and more appreciated in recent years, and a number of problems of taxonomic dispute has been solved through them. They help so much in tracing the affinities that, frankly speaking, all the assumed phylogenetic lines remain imperfect without their help.

It has already been mentioned that a number of wild species of these genera, viz., *Eleusine, Setaria* etc. occurs as wild in Indian plains. It is obvious that these wild forms, taken together with their cultivated relatives, form a very ideal problem for cytogenetical studies. In addition, the possibilities of such studies are further enhanced in the presence of a number of polyploid forms too. The genus *Sorghum* with all its species has recently been investigated in this laboratory and considerable facts of fundamental importance have been recorded. The present investigation with members of *Eleusine, Setaria* and *Pennisetum* were so undertaken hoping that here too, similar results might be obtained.

MATERIALS INVESTIGATED

The present investigation was carried out with several of the millets common in India and a few related species, which occur as wilds, all belonging to the family Gramineae. The following species were worked out :

1. *Eleusine indica* Gaertn.
2. *Eleusine coracana* Gaertn.
3. *Eleusine aegyptiaca* Desf.
4. *Setaria italica* Beauv.
5. *Setaria verticillata* Beauv.

6. *Setaria glauca* Hochst.
7. *Pennisetum typhoideum* Rich.
8. *Pennisetum orientale* Rich.

The species of *Eleusine aegyptiaca, E. indica* and *Setaria glauca* grow wild in the College compound, and so the materials could easily be collected. The species of *Eleusine coracana, Setaria italica, Pennisetum typhoideum* and *P. orientale* were grown in garden from the seeds obtained through the courtesy of Dr. L. S. S. KUMAR, Economic Botanist, Agriculture Dept., Govt. of Bombay. The seeds of *Setaria verticillata* were obtained through the courtesy of Prof. A. CAMARA, Director, Estacio Agronomica Nacional, Sacavem, Portugal.

In general, for somatic divisional stages, root-tips were collected from seeds and germinated in saw dust. In some cases, these were collected from plants growing in the pots. For meiotic studies, the plants were allowed to flower in the experimental plot and anthers collected in due time.

METHODS

For the study of somatic chromosomes from satisfactory preparations, trials in various fixatives had to be given. Various fixatives involving both metallic and non-metallic constituents were used with varying proportions of the constituents.

For species of *Eleusine coracana, E. aegyptica, Setaria glauca* and *S. italica,* fixation in paradichlorobenzene proved successful. Platinic chloride fixation was found essential in cases of *E. indica, P. orientale* and *S. verticillata.* In *Pennisetum typhoideum,* chromic-formalin fixative gave best results. After fixing the root-tips in definite proportion of the mixture of platinic chloride or chromic-formalin for overnight, they were washed in water for twenty-four hours and were subsequently embedded in paraffin after passing through alcohol and chloroform grades in the usual way.

For the somatic divisional stages of certain species, most satisfactory results were obtained by fixing the root-tips in saturated solution of paradichlorobenzene for about three hours in cold. Root-tips were then washed in water and heated in a mixture of 2% orcein and N.HCl in the proportion of 9 : 1 for about four to five seconds. Tips were then smeared in 1% aceto-orcein, applying uniform pressure.

For the fixation of flower buds, Belling's Navashin A and B in equal proportions were found to be most advantageous. The materials were pre-treated with Semmens's Carnoy's fluid (Absolute alcohol : Chloroform : Glacial acetic acid : : 3 : 1 : 1) for two to three seconds and then washed thoroughly in distilled water before fixation. Trials were also given in Karpachenko's fluid and Flemming's medium fluid.

For root-tips and flower buds, paraffin sections were cut at a thickness of 14μ and 16μ respectively. The slides were stained following the usual schedule of Newton's crystal violet-iodine technique.

Thirty seconds iodine-mordant instead of forty-five seconds was found to be very effective in case of flower buds. An overnight premordanting in 1% chromic acid proved to be essential in case of root-tips.

The figures were drawn at a table magnification of approximately × 3600 times using a Leitz Compensating eye-piece × 20 and an 1.3 apochromatic objective with an aplanatic condenser of 1.4 N.A.

Observations

All the millets and their related species investigated here reveal a general uniformity and similarity amongst the related members so far as their chromosome morphology and size are concerned. The species of *Eleusine* and *Setaria* have the chromosome numbers as multiple of nine. The species of *Pennisetum* reveal their basic number as seven.

Detailed morphology of the chromosomes of each species is given below :

1. *Eleusine indica* Gaertn. (2n = 18).

The somatic chromosome number of this species has been found to be 2n = 18. In general, it can be stated that there is no remarkable size difference in the chromosomes (from 1 μ to 2.4 μ). The following morphological observations could be made (figs. 1, 2) :

a) one pair of long chromosomes, each with a submedian primary constriction and a satellite with a long stalk on the longer arm;

b) one pair of long chromosomes with primary and secondary constrictions, one in median position, and the other at the end of one of the arms;

c) six pairs of medium sized chromosome with median primary constrictions;

d) one pair of short chromosomes with median primary constrictions.

2. *Eleusine coracana* Gaertn. (2n = 36).

The somatic chromosome number has been determined to be 2n = 36. Unlike the former species *E. indica,* size differences in the chromosomes are noted (from 1.2 μ to 2.4 μ). Due to size differences in the set, the chromosomes can be divided into three groups (fig. 3):

a) four pairs of long chromosomes;

b) twelve pairs of medium sized chromosome;

c) two pairs of short chromosome.

The detailed morphology could be worked out as follows (fig. 4):

a) two pairs of long chromosomes with primary and secondary constrictions, one in median position and the other near the end of one of the arms;

b) two pairs of long chromosomes with submedian primary constrictions and satellites on the shorter arms;

c) twelve pairs of medium sized chromosome with median primary constrictions;

d) two pairs of short chromosome with median primary constrictions.

Figs. 1 and 2. — *Eleusine indica* (2n = 18), somatic metaphase and idiogram respectively.

Figs. 3 and 4. — *Eleusine coracana* (2n = 36), somatic metaphase and idiogram respectively.

Figs. 5-7. — *Eleusine aegyptica* (2n = 45), somatic metaphase, (2n = 45), somatic metaphase, idiogram and meiotic stages respectively.

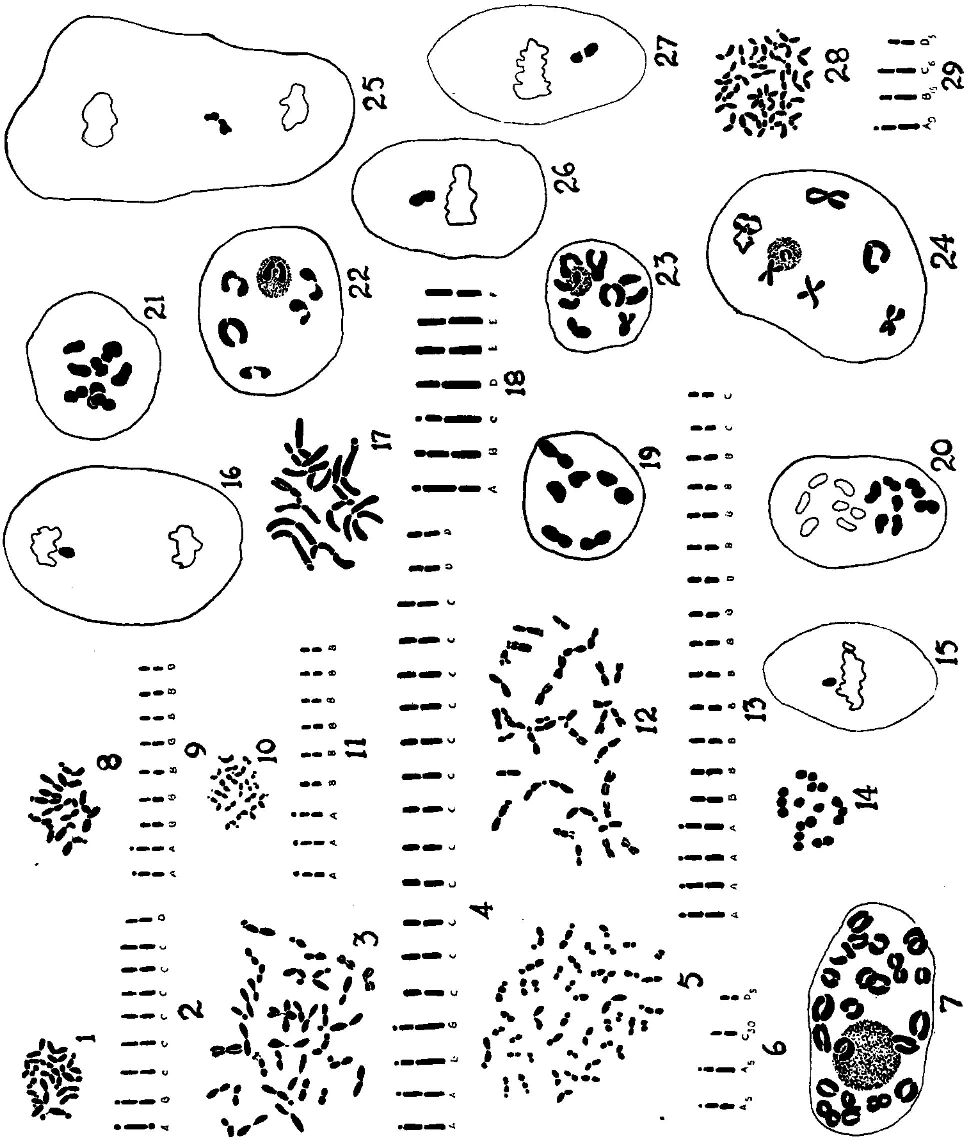
Figs. 8 and 9. — *Setaria italica* (2n = 18), somatic metaphase and idiogram.

Figs. 10 and 11. — *Setaria verticillata* (2n = 18), somatic metaphase and idiogram respectively.

Figs.12-16. — *Setaria glauca* (2n = 36), somatic metaphase, idiogram and meiotic stages respectively.

Figs. 17-27. — *Pennisetum typhoideum* (2n = 14), somatic metaphase, idiogram and meiotic stages respectively.

Figs. 28 and 29. — *Pennisetum orientale* (2n = 35), somatic metaphase and idiogram.



3. *Eleusine aegyptiaca* Desf. (2n = 45).

The somatic chromosome number of this species has been found to be 2n = 45. Like *E. coracana,* size differences are noted (from 0.9 μ to 2.1 μ), and as such, the chromosomes could be divided into three groups as follows (fig. 5):

a) five pairs of long chromosome;

b) fifteen pairs of medium sized chromosome;

c) five short chromosomes.

The detailed morphology could be worked out as follows:

a) ten long chromosomes with secondary constrictions, five of them with median primary constrictions and the other five with submedian primary constrictions and satellites on the shorter arms;

b) thirty medium sized chromosomes with nearly median primary constrictions;

c) five short chromosomes with median primary constrictions.

The first meiotic division of the P.M.C.s revealed twenty-one clear bivalents with one trivalent in diakinesis stage (fig. 7).

4. *Setaria italica* Beauv. (2n = 18).

The somatic chromosome number of this species has been determined to be 2n = 18. There is no remarkable difference in the size of the chromosomes (from 1.5 μ to 1.9 μ), yet the chromosome set may be grouped into two distinct groups as follows (figs. 8, 9):

a) two pairs of chromosomes with median primary constrictions and subterminal secondary constrictions;

b) seven pairs of chromosomes with median primary constrictions.

5. *Setaria verticillata* Beauv. (2n = 18).

The somatic chromosome number of this species has been determined to be 2n = 18, like the above-mentioned species of *Setaria italica.* In the shape, number and size of the chromosomes (from 9.6 μ to 1.9 μ) this species resembles *Setaria italica.* Two groups of chromosomes are as follows (figs. 10, 11):

a) three pairs of chromosome with median primary constrictions and satellites at the end of one of the arms;

b) six pairs of chromosome with median primary constrictions.

6. *Setaria glauca* Hochst. (2n = 36).

The somatic chromosome number of this species has been found to be 2n = 36. Unlike the other two species of *Setaria,* a bit noticeable size difference of the chromosomes has been revealed, size difference being 0.9 μ to 2.7 μ. From their detailed karyotype, the following three groups of the chromosome set could be worked out (fig. 12):

a) four pairs of long chromosome;

b) twelve pairs of medium sized chromosome;

c) two pairs of short chromosome.

On the basis of the nature of primary and secondary constrictions, the following karyotype could be worked out (fig. 13):

a) four pairs of long chromosome with nearly median primary constrictions and secondary constrictions at the end of one of the arms;

b) twelve pairs of medium sized chromosome with median primary constrictions;

c) two pairs of short chromosome with median primary constrictions.

The first meiotic division of the P.M.C.s showed eighteen clear bivalents at metaphase (fig. 14) in the polar view. Normal disjunction, together with early separation of one bivalent and lagging univalent, was also noted in some of the cases (figs. 15 and 16).

In several of the cases, secondary association of the bivalents in the first meiotic metaphase has been noted. Various sorts of groups could be recorded. The maximum association, i. e., the least number of groupings was found to be seven (fig. 14). - 2 (4) + 2 (3) + 1 (2) + 2 (1). The different types of associations are given below:

a) 1 (4) + 3 (3) + 5 (1)

b) 1 (6) + 1 (3) + 2 (2) + 5 (1)

c) 2 (4) + 2 (3) + 1 (2) + 2 (1)

d) 1 (4) + 2 (3) + 3 (2) + 2 (1)

e) 1 (3) + 5 (2) + 5 (1)

7. *Pennisetum typhoideum* Rich. (2n = 14).

The somatic chromosome number has been determined for this species to be 2n = 14. According to size differences of the chromosome set, it can be grouped into two:

a) six pairs of long chromosome;

b) one pair of medium sized chromosomes.

The range of size varied from 2.9 μ to 4.0 μ.

From an analysis of their detailed karyotype, the somatic chromosomes can be classified into the following morphologically distinguishable types (figs. 17, 18):

Type A — A pair of long chromosomes with submedian primary constrictions and each having a satellite at the longer arm.

Type B — A pair of long chromosomes with submedian primary constrictions and each having a secondary constriction placed submedian to the shorter arm.

Type C — A pair of long chromosomes with submedian primary constrictions each having a satellite to the shorter arm.

Type D — A pair of long chromosomes with submedian primary constrictions.

Type E — Two pairs of long chromosome with median primary constrictions.

Type F — A pair of short chromosomes with median primary constrictions.

The first meiotic metaphase revealed seven clear bivalents in the polar view (fig. 19). Normal anaphasic separation could be noticed with seven chromosomes in each pole (fig. 20). Together with this normal behaviour, several abnormalities were also noted as follows:

a) only six bivalents instead of seven in diakinesis (fig. 22).

b) eight bivalents in place of seven bivalents in both metaphase and diakinesis (figs. 21, 23, 24);

c) non-disjunction of one bivalent in side view (fig. 27);

d) early separation of one bivalent in side view (fig. 26);

e) anaphase showing one lagging bivalent in side view (fig. 25).

8. *Pennisetum orientale* Rich. (2n = 35).

The somatic chromosome number of this species is determined to be 2n = 35. Slight size difference is noted which varies between 1.0 μ to 1.7 μ, and the chromosomes are smaller than those of *P. typhoideum.* The chromosome set can be grouped into two categories which are as follows (figs. 28 and 29):

a) thirty-five long chromosomes;

b) five short chromosomes.

Detailed analysis of the karyotype, though could not be brought out, the following morphological types could easily be recognised.

Nine long chromosomes are with submedian primary constrictions and with satellites on the shorter arm. Fifteen long chromosomes are with submedian primary constrictions. Six long chromosomes are with median primary constrictions. Five short chromosomes are with median primary constrictions.

Discussion

Genera comprising the members of the millet complex fall under different tribes of the family Gramineae. Of the three genera investigated here, viz., the *Eleusine,* the *Setaria* and the *Pennisetum,* the latter two fall under Paniceae, and the former under Eragrostreae in Hutchinson's system of classification. The two tribes, however, in taxonomic classification, have been assigned positions one after the other. Eragrostreae has been placed following Paniceae.

The chromosome numbers so far reported in species of *Eleusine* are 2n = 18, 36, 45, etc., all being multiples of nine. The cultivated *Eleusine,* viz., *E. coracana,* commonly known as Ragi, possesses thirty-six chromosomes in the body cells and is regarded as a tetraploid. Krishnaswamy observed thirty-nine chromosomes in a variety viz., var. *tocussa* of *E. coracana.* The diploid numbers so far noted are all found in wild condition, mostly in different parts of the tropics. The only pentaploid species so far recorded is *E. compressa* noted by Krishnaswamy. *E. lagopoides* is the tetraploid form found wild in India.

The present work on the three species of *Eleusine* including both cultivated and wild forms corroborates the previous reports of chromosome numbers in *E. indica* and *E. coracana.* The demonstration of forty-five chromosomes in *E. aegyptiaca,* done in this report for the first time, adds another wild species in the list of polyploids so far recorded.

Of the genus *Setaria* of the Paniceae complex, a number of species, both high polyploids and diploids, have been recorded till now. *Setaria italica,* which is commonly cultivated in India as one of the millets, possesses eighteen chromosomes in the diploid set. This is in contrast to that of *Eleusine,* where the cultivated one is a polyploid. Most of the wild relatives, so far recorded, are either tetra or octoploids. The members of the genus grow both in the tropics and temperate regions, some of them being entirely cosmopolitan. The three species investigated here, viz., *S. italica, S. verticillata* and *S. glauca* show eighteen, eighteen and thirty-six chromosome numbers in the body cells respectively, corroborating the previous reports.

The genus *Pennisetum,* as far as the records reveal, indicates the presence of both X = 7 and 9 chromosomes in the basic set. The cultivated one, viz., *P. typhoideum,* commonly known as « Bajri », is cultivated in the plain throughout the upper and southern India. This is a diploid one with fourteen chromosomes, triploid forms being reported by Krishnaswamy. All the other cultivated species are either diploids, tetraploids, pentaploids or hexaploids. *P. typhoideum,* investigated here, reveals the presence of fourteen chromosomes as reported previously. In *P. orientale,* thirty-five chromosomes have been reported in the present work, thirty-six being reported by Avdulov in 1928. A variety, viz., *P. orientale,* var. *triflorum* shows forty-five chromosomes according to Krishnaswamy.

From a glance into the chromosome numbers so far reported in different wild and cultivated species of these genera, as well as taking into consideration the present observation, the role of polyploidy in the differentiation of the forms is obvious. In certain cases, it may be noted that the cultivated ones are diploid, while in others, they are polyploids. In cases where the cultivated types are polyploids, it is possible that they are the possible descendants of the wild diploid progenitors. Such types are best exemplified in case of *E. coracana.* The chromosome number in this species is thirty-six, whereas the wild species show both eighteen and forty-five chromosomes. The data uptil now recorded indicate that eighteen chromosomes of *E. indica* represent the normal diploid stage. The thirty-six chromosomes of *E. coracana* as reported by Krishnaswamy indicate the presence of groupings of bivalents in meiotic metaphase. The frequency chart presented by him shows a maximum of nine groups. If the theory of secondary association as a means of deriving the basic number of species is assumed to be correct, nine should be considered as the original haploid complement in the genus, at the same time indicating the secondary polyploid nature of *E. coracana*.

Another polyploid species, *E. aegyptiaca* with forty-five chromosomes, reported in the present paper, shows regular bivalent formation during meiosis. Occasional trivalents too are not of infrequent occurrence. The formation of bivalents during meiosis precludes the possibility of the species being an autopolyploid.

Taking all these facts into consideration, it seems quite likely that evolution within the genus *Eleusine* is mainly limited by allopolyploidy. From the diploid types growing wild, it may be assumed that through random interspecific crosses supplemented by polyploidy, species like *E. aegyptica* have evolved. As far as *E. coracana* is concerned, no doubt the intermixture of genomes as well as the duplication of satellites are involved in their evolution. It is not possible at the present state of our knowledge to state which of these phenomena preceeded the other, and which of these have taken place during cultivation. However, continued cultivation and judicial selection of this species have helped in their stabilization.

The role of polyploidy in evolution within the genus *Setaria* is also obvious. The cultivated one is a diploid type, whereas the wild species, viz., *S. glauca* is polyploid. A number of diploid as well as polyploid species are also on record in the works of different workers. It is an interesting fact that most of the cultivated species are diploids. The species *S. verticillata* received from Portugal too shows 2n = 18 forms. It is, therefore, definite that cultivated types like *S. italica* are derived from some wild diploids not yet thoroughly known.

The origin of high polyploid species like *S. glauca* with 2n = 36 chromosomes also indicate the role of allopolyploidy in its evolution. This is an assumption based on the occurrence of groupings of bivalents of the first meiotic metaphase stages in several of the P.M.C.s. In most cases they are aggregated into nine groups of bivalents. This no doubt shows that the origin from these forms involves interspecific crosses between species, having nine as the basic set of chromosomes. Nine may, therefore, be confidently claimed as representing the basic set from which different species have been derived in evolution. The presence of univalents too support this hybrid origin.

As far as the genus *Pennisetum* is concerned, the cultivated species is a diploid with 2n = 14 chromosomes and wild species, such as *P. orientale*, has been recorded with thirty-five chromosomes in the somatic set. In this case the role of polyploidy even within the cultivated type is evident in the occurrence of twenty-one chromosomes in one of the forms of *P. typhoideum*. The number thirty-five recorded in the present investigation in *P. orientale* also suggests its origin from types with seven chromosomes. It is interesting to note that Krishnaswamy reports a variety of *P. typhoideum* with forty-five chromosomes. It, therefore, seems quite likely that the polyploid types showing chromosome number as multiples of nine are the derivatives from the species having seven in basic set.

The karyotype analysis so far performed in the different genera as well as their constituent species show marked similarity in their morphology between the members of the same genus. This is quite likely if one assumes a homogeneous line of evolution within each individual genus. The resemblances in chromosome morphology between different genera are, however, not so striking as to indicate the affinities of one with the other.

Interpretation of the meiotic irregularities noted in *P. typhoideum*

It is apparent from the text that in addition to non-disjunction and lagging of chromosomes, a number of P.M.C.s. have been noted in *P. typhoideum* with twelve or sixteen chromosomes in the pollen mother cells. As the somatic cells show perfect regular behaviour, it is quite likely that the occurrence of such abnormal P.M.C.s are the result of irregularity in chromosome behaviour involving non-disjunction of chromatids at the pre-meiotic stage, as noted in case of *Datura* by Bhaduri and Sharma (1946). Such premeiotic irregularities can easily be visualized to give rise to P.M.C.s with sixteen, fourteen and such other irregular numbers of chromosomes. If these cells can form viable gametes their importance in evolution is immense and the occurrence of trisomic and tetrasomic are then expected in nature. The occurrence of species with chromosome numbers as multiples of nine may also be assumed to have originated through such processes operating in species having chromosome number as multiples of seven. A thorough research in this direction is highly desirable.

SUMMARY

1. A cytological investigation of the somatic chromosomes of eight different species of Gramineae, including the common millets and the related species has been carried out. The following are the names of the species investigated :

1. *Eleusine indica* Gaertn. (2n = 18),
2. *Eleusine coracana* Gaertn. (2n = 36),
3. *Eleusine aegyptiaca* Desf. (2n = 45),
4. *Setaria italica* Beauv. (2n = 18),
5. *Setaria verticillata* Beauv. (2n = 18),
6. *Setaria glauca* Hochst. (2n = 36),
7. *Pennisetum typhoideum* Rich. (2n = 14),
8. *Pennisetum orientale* Rich. (2n = 35).

Somatic chromosome of these have been worked out in details, and meiosis hase been studied in *E. aegyptiaca, S. glauca,* and *P. typhoideum.*

2. The species of *Eleusine* and *Setaria* show the chromosome numbers as multiples of nine (x = 9). The species of *Pennisetum* reveal their basic number as seven (x = 7). Meiotic irregularities have been found to be common in *S. glauca* and *P. typhoideum,* secondary association being noted in the former species.

3. Taking into account the previous data on the cytology of the species as well as the data of the present investigation, each genus is supposed to represent a homogenous line of evolution.

4. The role of polyploidy in speciation in each of the genera is discussed. Cultivated as well as wild types have been assumed to have originated through allopolyploidy.

5. The resemblances in chromosome morphology between different genera are, however, not so striking as to indicate the affinities of one with the other.

6. The implications of meiotic irregularities noted in *P. typhoideum* are discussed.

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RIASSUNTO

È studiato il cariogramma di alcune Graminaceae della flora indiana: *Eleusine indica* Gaertn. (2n = 18), *Eleusine coracana* Gaertn. (2n = 36), *Eleusine aegyptiaca* Desf. (2n = 45), *Setaria italica* Beauv. (2n = 18), *Setaria verticillata* Beauv. (2n = 18), *Setaria glauca* Hochst. (2n = 36), *Pennisetum typhoideum* Rich. (2n = 14), *Pennisetum orientale* Rich. (2n = 35). Il numero base delle specie di *Eleusine* e di *Setaria* è pertanto x = 9; quello delle specie di *Pennisetum* x = 7. Sono state osservate irregolarità meiotiche in *Setaria glauca* e *Pennisetum typhoideum* con associazione secondaria in quest'ultima specie. Ogni genere appare come il rappresentante di una linea omogenea di evoluzione, nella quale le specie a più elevato numero cromosomico, sia selvatiche sia coltivate, sono originate per allopoliploidia. La morfologia cromosomica dei differenti generi non fornisce indicazioni circa la loro reciproca affinità.