Verfahren nachweisen, und zwar durch einen direkten Vergleich der durchschnittlichen Hypokotyldurchmesser von Pflanzen aus großen und aus kleinen Samen mit Hilfe des t-Testes. Zu diesem Zweck wurden 2 Gruppen gebildet: Pflanzen aus Samen der Sortierungen über 1,5 mm und solche aus den Saatgutfraktionen unter 1,5 mm. Das arithmetische Mittel des Hypokotyldurchmessers der 1. Gruppe beträgt 34,0 mm, das der 2. Gruppe 28,6 mm. Die Differenz von 5,4 mm ist für P = 0,1% signifikant (GD = 2,0 mm).

Um zu prüfen, ob der Ernährungszustand der Mutterpflanze auch unabhängig von der Samengröße einen Einfluß auf die Hypokotylverdickung der Tochterpflanzen ausübt, wurden die Werte des durchschnittlichen Hypokotylrübendurchmessers beider Nachkommenschaftsgruppen für die verschiedenen Siebsortierungen mit Hilfe der Differenzmethode verglichen. Für die Differenz ergibt sich ein t-Wert von 0,89 (der Tabellenwert für P = 5% beträgt 2,37). Eine Überlegenheit der Nachkommen besser ernährter Samenträger ist somit nicht nachweisbar. Eine Tendenz in der erwarteten Richtung zeigen lediglich die beiden niedrigsten Fraktionen der Samengröße, die sich bereits in der Keimfähigkeit abweichend verhielten. Hier treten auch in der Hypokotylbreite bei den Nachkommen normal ernährter Pflanzen höhere Durchschnittswerte auf als bei den Nachkommen der Hungerformen; die Differenzen von 5,5 bzw. 3,7 mm sind jedoch nicht signifikant.

Im weiteren Verlauf der Vegetationsperiode bildeten auch die zunächst schwach entwickelten Pflanzen durch anhaltendes sekundäres Dickenwachstum des Hypokotyls beträchtliche Speicherorgane aus. Vorzeitiges Schossen trat in diesem Versuch, bei dem stets für ausreichende Bodenfeuchtigkeit gesorgt wurde, nicht ein.

Zusammenfassend kann gesagt werden, daß die von E. BAUR beschriebenen extremen Nachwirkungen des Hungerzustandes der Mutterpflanze auf die Tochtergeneration bei den von uns verwendeten Sorten und Versuchsbedingungen nicht zu beobachten waren. Wohl aber konnte der Einfluß des Nährstoffvorrates im Samen über die Jugendentwicklung auf die weitere Ausbildung der Tochterpflanzen, besonders in ihren nährstoffspeichernden Teilen, nachgewiesen werden. Dieser Zusammenhang ist jedoch bereits seit längerer Zeit für zahlreiche Kulturpflanzen bekannt (vgl. z. B. STAFFELD 1926). Es ist möglich, daß bei bestimmten Radiessorten mit der schwächeren Hypokotylentwicklung von Pflanzen aus Kümmersamen auch ein vorzeitiges Schossen verbunden ist. Als „Schulbeispiel" für Dauermodifikationen erscheint aber die Hungerform des Radieschens nicht sehr geeignet, zumal die Wirkung in keinem Fall über mehrere Generationen hinwegreicht.

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Cytogenetic evidence of relationship between the X-7 and X-9 groups of *Pennisetum* species*

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With 1 figure

1. Introduction

Cytologically and morphologically the genus *Pennisetum* consists of two groups of species, one with a basic chromosome number of x = 7, the other with x = 9. Although the possibility of cytogenetic affinities between the tall penicillate anthered mesophytic group with x = 7 chromosomes and the much smaller, mostly smooth anthered, widely occurring x = 9 group has long been of interest to cytogeneticists, no experimental evidence for this has been obtained to date. Thus, HRISHI (1952) reports complete failure of hybridization between species of the two groups[1]. However, during 1949, following an extensive crossing programme between perennial *Pennisetum dubium*, which is an irregular high polyploid showing close morphological affinity to the x = 9 group, and *P. typhoides* (2n = 14), which is a regular annual diploid of the x = 7 group, the senior author was able to produce a single hybrid plant. It is the purpose of this paper to describe the cytogenetic behaviour of this hybrid and to demonstrate that some cytogenetic affinity exists between these two groups of species which are, morphologically, so different.

2. Materials and Methods

In perennial *P. dubium* chromosome numbers may vary from 14 to 84 in cells of the same root tip, from 47 to 74 at MI and from 9 to 37 at MII of the same anther. The most frequent number, both in mitosis and at MI is 2n = 66, but at MII there is an abnormal reduction in chromosome number, so that 97% of the cells contain less than the expected n = 33 chromosomes (GILDENHUYS and BRIX, 1958).

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[1] Since this paper was written it has come to our notice that a hybrid between *P. typhoides* and *P. squamulatum* (2n = 54) has been produced — Nature 189, 419—420 (1961).

Polyploidy in the species is maintained by facultative aposporic apomixis (GILDENHUYS and BRIX, 1959). As pointed out previously, this species bears a close morphological resemblance to the x = 9 group of species, although its odd cytological behaviour suggests that it might be of hybrid origin, possibly even a hybrid between x = 7 and x = 9 individuals (GILDENHUYS and BRIX, 1958). Using pollen from this species, some thousands of pollinations were made onto the annual regular diploid *P. typhoides* (2n = 14). Only a single perennial hybrid plant was obtained from these crosses. This was divided clonally and planted in the field for observation.

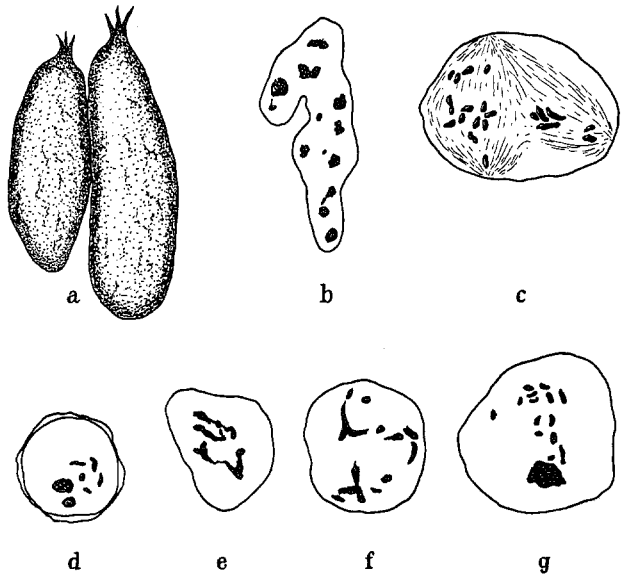

Fig. 1. Abnormalities in the hybrid *P. typhoides* × *P. purpureum*. — a) Markedly unequal antherlobes; b) Plasmodium with many nuclei; c) Tripolar spindle at AI; d) Young pollen grain with micronuclei and chromosomes; e)+f) Sticky chromosomes at MI (e) and MII (f); g) TI with only one organised nucleus and laggards. Eulargement: 1 a×60, 1 b×240, 1 c—g×600

3. Observations

Morphologically the hybrid plant resembles the tall penicillate anthered mesophytic x = 7 group and, except for its perennial habit, it shows no resemblance to its polyploid perennial parent.

It has 21 chromosomes, so that it received only 14 from its polyploid parent. Although in two cells out of 153 chromosome numbers of 24 and 25 were encountered, none of the characteristic mitotic abnormalities of the polyploid parent occurred. In contrast, microsporogenesis exhibited the full range of abnormalities as described for *P. dubium* (GILDENHUYS and BRIX, 1958). In addition, some other gross abnormalities were encountered. Thus, the two anther lobes were sometimes markedly unequal in size (Fig. 1a), while in many anthers P.M.C.'s appeared to be absent. Some anther lobes contained only masses of cytoplasm with free nuclei (Fig. 1b), while in others these plasmodia occurred in varying proportions with P.M.C.'s. Sectioned material showed that plasmodia are not limited to any particular region of the anther and that they vary considerably in size and in the number of nuclei they contain. It was impossible to follow any sequence of meiotic divisions in plasmodia; invariably the nuclear divisions were synchronous, showing from a few to many chromosomes, but in most cases the number was 21. No pairing of chromosomes occurred and the divisions appeared to be purely mitotic.

P.M.C.'s varied in size and, as in the polyploid parent, they showed evidence of abnormal premeiotic mitoses. Thus they often had more than one nucleus and/or micronucleus. The occurrence of sticky chromosomes (Fig. 1 e & f), made it difficult to determine whether certain of the groups of chromosomes were of the type occurring in mitosis in the polyploid parent, whether they were due to homologous associations or whether they were merely the result of stickiness. However, in many cells which showed no evidence of stickiness, no pairing occurred at early prophase (51 cells) nor could any evidence of pairing or chiasmata be found in diakinesis (27 cells) or MI (50 cells). It must be assumed, therefore, that no chromosome pairing occurs at meiosis in this hybrid. The chromosome number varied from 21 to 42, but was almost invariably 21 (Table 1).

Table 1. *Frequencies of P.M.C.'s with different chromosome numbers in the hybrid P. typhoides × P. dubium*

Chromosome number	21	22	24	25	26	27	31	40	42	Total
No. of P.M.C.'s	106	1	1	1	1	1	1	2	3	117

At AI the chromosomes usually did not divide, but migrated, undivided, to the poles, resulting in distributions varying from 17:4 to 10:11. In a few cases (6.5%) all chromosomes divided, apparently in a mitotic manner, and yet in other cases some divided, others not. Lagging was evident in most first divisions. At AII individual chromosomes migrated divided or undivided and the distribution was often grossly unequal. After the second division the overall mean number of chromosomes per cell was 5.5 undivided and 1.3 divided. A few cells contained as low a number as one undivided and one divided chromosome, while two cells were found to contain as many as 17 undivided chromosomes. Normal tetrad formation did not take place and pollen grains, when formed, frequently contained only micronuclei and individual chromosomes (Fig. 1 d). The mature grains were shrivelled and were not shed from the anthers.

A noteworthy feature during meiosis was the lengthy delay in the organisation of new nuclei. At TI one nucleus was often organised, whilst at the other pole no sign of a nucleus initial could be observed and some of the chromosomes were still lagging on the spindle (Fig. 1 g). After second division, in many cells, there was still no indication of an organised nucleus at the time that the nucleolus appeared, or even by the time that the exine had been formed around the pollen grain.

In 95.5% of 200 ovules examined, no embryo sacs could be found; the remainder were all eight nucleate and they appeared to have arisen meiotically. This low incidence of megagametogenesis is most likely due to a similar breakdown of meiosis as occurs during microsporogenesis and the failure to produce aposporic sacs might therefore be due either to the parental chromosome(s) and hence parental gene(s) responsible for aposporic embryo sac development not being present in the hybrid or to recessiveness.

4. Discussion

The mitotic and meiotic abnormalities in *P. dubium*, apart from sticky chromosomes at meiosis, are very similar and are genetically controlled (GILDENHUYS and BRIX, 1958). Further, clones showing a high percentage of abnormalities in mitosis also do so at meiosis. This leads to the supposition that similar mechanisms are involved and that this species demonstrates DARLINGTON's (1937) postulation, viz. that meiosis and mitosis are essentially similar phenomena and that "The special properties of meiosis follow from the precocity of the prophase and not from the action of new forces". In the hybrid, however, the position is somewhat different, for although meiotic abnormalities similar to those of the perennial parent are common, corresponding mitotic irregularities do not occur. It would seem, therefore, that whatever the genetic basis for these abnormalities, they may be initiated at different stages in the development of the individual, or that either (i) the gene(s) or gene complexes responsible for the abnormalities are not necessarily the same for mitosis and meiosis (cf. SACHS, 1952), or (ii) the cytoplasm of the hybrid is responsible for the differential expression of the genotype. It is significant to mention here that as soon as the chromosome number of the hybrid is doubled by means of colchicine treatment, the mitotic abnormalities of the polyploid parent re-appear, so that any possible cytoplasmic barrier to the expression of mitotic irregularities appears to be overcome by the presence of genes in double dosage. In fact, the re-appearance of these abnormalities makes it virtually impossible to procure an amphidiploid from the hybrid (GILDENHUYS and BRIX, 1961).

Failure of chromosome pairing at meiosis in the hybrid may possibly be due to one of two reasons. First, there may be little or no homology between the chromosomes received from the two parents. Secondly, the wide range of chromosome associations in the polyploid parent (from 27 univalents to complete pairing — GILDENHUYS and BRIX, 1958) suggests that in this species failure of pairing is due, in part at least, to genic control (cf. STEBBINS, 1951), so that the failure of pairing in the hybrid could be due to a similar cause. This is supported by the fact that in the few P.M.C.'s with more than 21 chromosomes, and in which some chromosomes must therefore have had homologues, no evidence of pairing was encountered. It can therefore be suggested that failure of pairing in the hybrid is due to genically controlled asynapsis.

STEBBINS (1951) has pointed out that "When extensive duplication of chromosomal material exists, as it does in such polyploids, regular behaviour of the chromosomes at meiosis is not essential to the production of viable gametes, since many different combinations of the various chromosomes can function." Now, it must be assumed from the fact that *P. dubium* requires pollination for seed formation (GILDENHUYS and BRIX, 1959), that many of its highly reduced microspores have the required combinations to be viable and to effect fertilization of at least the polar nucleus, thus bearing out the contention of STEBBINS. The important point in the present investigation is, however, that the particular chromosome combination capable of producing a viable embryo with *P. typhoides* was recovered only once from many thousands of highly reduced pollen grains. Furthermore, this gamete was one which, judging by the appearance of the hybrid (which does not resemble its polyploid parent), contained a genome(s) rather similar, though not necessarily homologous with at least one of the genomes of the x-7 group.

P. dubium, as pointed out, shows close morphological affinity to the x = 9 chromosome group of *Pennisetum* species, and although it might even be a hybrid between a x = 7 and a x = 9 species as has been suggested, it nevertheless has close relationship with this group. It may form a bridging species between the two groups, but whatever the explanation and in spite of past failures to hybridize species of the two chromosome groups, sufficient cytogenetic affinity exists between the two groups to permit the very rare formation of a hybrid.

5. Summary

1. The genus *Pennisetum* consists, cytologically and morphologically, of two groups of species, one with x = 7, the other with x = 9 chromosomes.

2. A single sterile perennial hybrid plant was produced by using pollen from the irregular, high polyploid *P. dubium*, which is a perennial resembling the x = 9 group morphologically and the regular annual diploid *P. typhoides* (2 n = 14) of the x = 7 group.

3. The hybrid, with 2n = 21, received only 14 chromosomes from its irregular polyploid parent and it does not resemble the x = 9 group of species but bears strong morphological resemblance to the x = 7 group.

4. The cytology of the hybrid is described. It shows gross abnormalities in addition to the ones also exhibited by *P. dubium*. Failure of chromosome pairing is attributed to genic control.

5. Although *P. dubium's* morphological affinities lie with x = 9 group of species, it has been possible to recover a rare gamete having the chromosome number and affinities of the x = 7 group in the hybrid, thus demonstrating some cytogenetic affinity between the x = 7 and x = 9 groups of *Pennisetum* species.

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