To my children Farhad and Pardis

# The Cytology of *Eragrostis* with Special Reference to *E. tef* and its Relatives

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at the University of London

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Abstract

Thirty-seven species of the genus Eragrostis (Poaceae: Eragrostoideae) have been examined cytologically. Somatic chromosome numbers are reported for the first time for seven species. New chromosome numbers are reported for a further seven species. Counts confirming those obtained by previous authors were obtained for twenty-six species. An annotated list of all published counts for species of Eragrostis was compiled.

The base number for the genus is x=10. Many of the species contain two or more chromosome races. The frequency of polyploidy is high (76%). This is notable for a tropical genus. Aneuploids are relatively frequent (14%) and possible explanations are provided.

The karyotypes of fifteen species were studied. Most of them showed a gradation in the size of chromosomes whose centromeres were mostly median and submedian. Three species had karyotypes which were distinctly different, having shorter, fatter and less symmetrical chromosomes respectively.

All the varieties of the Ethiopian cereal Eragrostis tef examined were tetraploid, with regular meiosis. Hybrids between t'ef varieties of very different appearance were fertile and formed only bivalents in meiosis, but hybrids between tetraploid E. cilianensis and tetraploid E. minor were sterile, having abnormal meiosis with many univalents.

Pollen diameter was found not to be a reliable indicator of chromosome number.

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# CHAPTER 1

# GENERAL INTRODUCTION

## 1.1 Historical Introduction

Eragrostis is a genus of grasses confined to the warmer parts of the globe. It is one of the largest genera of the subfamily Eragrostoideae: according to Airy-Shaw (1966) it has 300 species. Eragrostis species are characteristic of semi-arid or arid climates but few are major components of natural vegetation. Only two of them are of some economic importance: Eragrostis curvula, an important pasture-grass in U.S.A. and elsewhere, and E. tef, a cereal in the highlands of Ethiopia and a fodder-crop in South Africa.

There have been few extensive studies of Eragrostis. Clayton's taxonomic account of East African species (1974), using characters observable in the herbarium, has revealed something of the taxonomic complexity of those species. The largely unpublished account by Ponti (1978), using mainly obscure morphological and anatomical characteristics, has established affinities between some of the species she studied as live plants. Apart from these and some less important studies, we know relatively little about the systematics of this genus. On geographical and

morphological grounds (Hartley and Slater, 1960; Stebbins, 1956) the Eragrostoideae are relatively archaic. The Eragrosteae in particular are unspecialised and, since the grains of Eragrostis species are shed naked (a most unusual feature in wild grasses), this genus may be the most primitive in the subfamily (B.M.G.Jones, verbal communication).

The nuclear cytology of Eragrostis has not been examined systematically to any large extent before. Pienaar (1953, 1955) studied mitosis and meiosis in seventeen perennial South African species, several of which belonged to the E. curvula aggregate.

Behind many of the published counts is the problem of taxonomic uncertainty as to whether the plants were correctly identified. Much Botanic Garden material of Eragrostis is incorrectly named and even experienced and acknowledged experts in the taxonomy of the genus admit that the discrimination and identification of species is often difficult (W.D.Clayton, informal communication).

Even less is known about the genetics of the genus. Apart from studies of crosses between elements of the E. curvula - lehmaniana - chloromelas complex (Busey, 1974; Voight, 1984) and some hybridizations between lines of E. tef (Tareke, 1976 and 1981) virtually nothing is known about the genetic relationships of species of the genus.

Eragrostis tef is the crop plant whose failure led to the Ethiopian famines of the early 1970's and 1980's. It has considerable potential as a cereal for the semi-arid tropic. Nevertheless, t'ef has been studied little. It was not recognised as chasmogamic until 1974 (Tareke, 1981) and its nearest wild relatives were only recognised in 1978 (Jones, Ponti, Tavassoli and Dixon). However, Hackel (1887) considered E. tef as a cultivated form of E. pilosa. A concerted effort towards its improvement has yet to be made, but Tareke Berhe made a number of crosses between 1976 and 1981. This work has been continued by Seyfu Ketema, who made a special study of lodging and hybridization technique in the species (1983).

This thesis reports cytogenetical investigations made between 1975 and 1979 which were intended to throw light on the relationship between t'ef and other species of Eragrostis, and incidentally upon other relationships in the genus. It is my contribution to the t'ef studies carried out at Royal Holloway College by B.M.G.Jones, J.A.Ponti (1974-8), Seyfu Ketema (1980-3) and myself (1975-9 and 1984-5).

The results of my chromosome studies, both mitotic counts and meiotic observations, are given in Chapter 2 of this thesis. Karyotype studies are described in Chapter 3. The results of an investigation of pollen

grain size, to see whether it is of value as an indicator of chromosome number, are given in Chapter 4. Chapter 5 gives an account of my hybridization experiments and some general conclusions resulting from my studies are given in the final chapter. All reported chromosome numbers for Eragrostis species are given in Appendices 1 and 2.

## 1.2 Materials and methods of cultivation

The seeds of the Eragrostis species studied in this work were supplied by Botanic Gardens in Africa and Europe, and by Research Institutions in Africa and America. Seeds of some Eragrostis species were supplied by people who had collected them from the wild. The seed accession numbers and the names of suppliers are listed in Appendix 3.

The seeds were sown in 9cm size plastic pots in John Innes Seed Compost, and kept in a glass-house. The seedlings were usually transferred to 13cm size pots and John Innes No.2 compost, when they were about 5cm high. One plant was grown in each pot and at least three plants of each accession number were grown to maturity. Occasionally so few seeds germinated that only one or two plants could be grown. Perennial species were transferred to larger pots after the first year. Plants were watered regularly, but special care was taken not

to over-water them during winter. The glass-house conditions under which the plants were grown were as follows:

1- The maximum temperature during the day in the summer months rarely rose above +30° C because of the automatic vents and the application of "Coolglass" glass-house shading. Nevertheless on exceptional days the temperature reached +36° C. The minimum temperature during summer nights was kept up to +10° C.

2- The minimum temperature during winter days was about +18° C and in practice the temperature was fairly constant at about +20° C. During winter nights, occasional minimum temperature as low as +6° C were recorded, but by using supplementary glass-house heating the night temperature was usually maintained at a minimum of +10° C.

3- Supplementary "Gro-Lux" lighting was provided during the winter to maintain a 12 hours day-length and to provide extra illumination during the hours of natural low-intensity day-light.

4- The maximum humidity recorded in summer was 94%RH and the minimum in summer was 71%RH.

5- The maximum relative humidity in winter was 90%RH and the minimum was 74%RH.

Accessions were maintained by sowing seed obtained in glass-house culture. To prevent cross pollination, one or two panicles of each plant were bagged and the mature seed gathered later.

Voucher specimens were made by collecting and drying mature plants. The dried specimens were identified by the present author and J.Ponti by comparison with specimens determined by staff of the Herbarium of the Royal Botanic Gardens, Kew and by comparison with published descriptions in floras (especially the accounts by Clayton, 1974 and by Gould, 1975). Critical material of two accessions was checked by Dr. Clayton for us. The voucher specimens are preserved in the herbarium of Royal Holloway & Bedford New College.

Some of the seeds which came from Botanic Gardens were wrongly named. Occasionally the packets of seed contained a mixture of more than one species and once, included interspecific hybrid seed (see Chapter 2 and 5). In these cases the seed accession numbers are followed by an alphabetical letter to indicate the different species.

# CHAPTER 2

# CHROMOSOME NUMBER

## 2.1 Introduction

The first chromosome numbers for Eragrostis species were reported by Avdulov (1928). Since then several authors have reported chromosome number for species of this genus. At the present time a total of 556 counts have been obtained, refering to no less than 120 species (see Appendix 1 and 2). Among the more notable contributors are Moffett and Hurcombe (1949), who reported the chromosome numbers for 22 Eragrostis species, and Pienaar (1953, 1955) reported the chromosome numbers for 17 species (one of which was not named). de Wet (1954, 1956, 1958 and 1960), Tateoka (1953, 1954a, 1954b, 1955, 1962, 1965a, 1965b, 1965c), Ono and Tateoka (1953), Gould (1958, 1960, 1964, 1965, 1966, 1968a, 1970), Gould and Soderstrom (1967, 1970 and 1974) and Mehra, Khosla, Kohli and Koonar (1968) have also made significant contributions to the chromosome numbers for Eragrostis species.

The chromosomes of Eragrostis species are very small, difficult to prepare for observation, and often numerous. There is thus some possibility of erroneous counts, especially among polyploids. For example, the

counts of 2n=35 for E. pilosa published by Sokolovskaya and Shelkova (1932) proved on reexamination to be 2n=40 (Sokolovskaya and Probatova, 1978). A similar error has been corrected for E. spectabilis: 2n=40, and not 42 (Nielson, 1939). Other counts reported may be erroneous, but undetected.

Difficulties in the identification of Eragrostis species are another problem: the count of 2n=40 for E. cilianensis published by Ono and Tateoka (1953), later on was refered to E. minor (Tateoka, 1955). Similarly the count of 2n=40 for E. pilosa reported by Ono and Tateoka (1953), later on was refered to E. multispicula (Tateoka, 1965c). Pohl (1980) reported that the count of 2n=40 for E. viscosa published by Gould and Soderstrom (1970a) refers to E. hondurensis. Such misidentification of Eragrostis species was greatest among the earliest counts, where material was often not identified by an expert and no voucher specimen was kept.

In this Chapter I report sixty-nine chromosome numbers for thirty-seven Eragrostis species. Seven of these counts refer to previously uncounted species and another seven are new numbers for species already cytologically examined. These and previously published counts are used to determine the base numbers for Eragrostis. The frequencies of polyploidy and

aneuploidy are reported and their origin is discussed. Meiosis is described for selected species which are related to t'ef.

## 2.2 Method

### 2.2.1 Mitosis

Root tips were used routinely for observations of somatic chromosome numbers. Sixty-nine accession numbers comprising thirty-seven Eragrostis species were studied. Root tips were collected mainly from pot-grown young plants. The root tips were collected from individual plant and where it was possible, at least three plants of each accession number were studied.

The root tips were treated with 0.2% aqueus colchicine solution for 2 hours, after which they were washed with distilled water and fixed in 3:1 absolute ethyl alcohol: glacial acetic acid mixture for twenty four hours. The root tips then were stored in 70% ethyl alcohol, in a freezer below -10° C. For staining the chromosomes, Feulgen solution was used. The root tips were first hydrolised in 1N HCl at +60° C for 10-12 minutes and then they were washed with cold distilled water. The stained part alone was squashed in a drop of 45% acetic acid under a binocular microscope.

A number 0 cover-glass was put on and the preparation tapped to disperse the cells. The cells were flattened by pressing the slides between a few layers of filter paper. Observations were made with a Leitz Dialux microscope. The photographs of mitotic chromosome preparations were then taken with an oil immersion objective (magnification x90) on Ilford Ilfodata micronegative film. Slides were made permanent, using solid CO2 to freeze them (method of Conger and Fairchild, see Darlington and La Cour, 1970). After freezing the cover-glass was lifted with a razor blade and both cover-glass and slide were put in 95% ethyl alcohol for 5 minutes. The slide and cover-glass were then transferred to absolute ethyl alcohol for 5 minutes. The preparations were finally made permanent by mounting them in Euparal.

Difficulties were experienced in making good preparations. Various improvements were attempted, including varying the time of collection of roots; cooling of root tips and pretreatment with monobromonaphthalene, the use of Newcomer's and Carnoy's as alternative fixatives; propiono-carmine, aceto-carmine and aceto-orcein as alternative stains; pectinase as an alternative macerant; phase-contrast as a supplement to staining. None of these gave better results than the method described above. Obtaining vigorous roots was a persistant problem, especially with

the tropical species of Eragrostis. It also proved to be difficult to flatten the cells sufficiently without breaking them, in order to obtain countable preparations. Comparable difficulties may account for the virtual absence of photographs of Eragrostis chromosomes in the published literature.

2.2.2 Meiosis

Observations of meiosis were made on pollen mother cells of the following Eragrostis species: E. aethiopica, E. bicolor, E. heteromera, E. mexicana, E. pilosa, three accessions of E. tef, E. minor and three hybrids (two synthetic and one naturally occurring hybrid). Spikelets from young panicles emerging from the sheath of the flag leaves, were fixed in 3:1, absolute ethyl alcohol:glacial acetic acid for twenty-four hours. The spikelets then were stored in 70% ethyl alcohol. Staining of the chromosomes was carried out by treating spikelets in the manner previously described for root tips. After staining, the anthers were removed with a needle from the florets of the spikelets under the binocular microscope. It was noticed that meioses were most frequent in those panicles which had emerged between one-third and two-thirds of their total length. In each species the size of the anthers which had pollen mother cells (P.M.C.'s) in division were about the same size as

anthers which had newly-formed pollen grains, which could be seen under the binocular microscope. It was found that, in a given spikelet, the floret which was above the floret with newly-formed pollen grains was the only one likely to have P.M.C.'s in division.

The number of P.M.C.'s in each anther varies from species to species in Eragrostis. Ponti (1978) showed that among the species studied P.M.C. numbers varied between 2 and 10 per loculus. This represents a low number of P.M.C.'s per anther and accordingly it was often difficult to find appropriate stages even when many preparations were studied. Eragrostis heteromera, which I also studied, had higher numbers of P.M.C.'s per anther.

Aceto-carmine, propiono-carmine and acetic-orcein were also used as alternative stains to Feulgen for meiotic preparations but did not give such good results. Occasionally, when Feulgen's stain did not stain intensely, irrigation with aceto-carmine intensified it.

The studies of meiosis were mainly confined to the months from May to September. Attempts to make preparations between October and April were unrewarding: flowering was irregular, anthers were often aborted and the plants lacked vigour.

## 2.3 Results

### 2.3.1 Mitosis

Somatic chromosome numbers were determined for sixty-nine accessions representing thirty-seven species of Eragrostis. Chromosome numbers, locality and the accession numbers of all species studied are given in Table 2.1.

Thirty-two species were found, in this study, to be represented by a single chromosome number: thirteen species had 2n=20, thirteen species had 2n=40, three species had 2n=60, one species had 2n=80, one species had 2n=58 and one species had 2n=41. Five Eragrostis species had more than one chromosome number among the different accessions: E. cilianensis had 2n=20, 40 and 60; E. minor had 2n=20 and 40; E. curvula had 2n=40 and 70; E. pectinacea had 2n=40 and 60 and E. tenuifolia had 2n=40 and 41.

Chromosome counts for seven Eragrostis species are reported for the first time. These species are: E. aethiopica, with chromosome number 2n=20; E. botryodes, with 2n=80; E. congesta with 2n=40; E. kiwuensis, with 2n=40; E. orcuttiana, with 2n=20; E. porosa, with 2n=40 and E. schweinfurthii with 2n=40. Mitotic preparations of some of these species are presented in Plate 2.1.

Table 2.1 Chromosome numbers of Eragrostis species determined by the present author

| Accession Number | Species | n | 2n | Country, Province and Locality |
|---|---|---|---|---|
| 75-1 | !E. aethiopica Chiov. | 10 | 20 | South Africa, Transvaal, Shingwidzi |
| 75-144 | E.aspera Nees | | 20 | Zimbabwe, Manicaland, Umtali, Uumba |
| 75-61 | E. atroviens (Desf.) Steud. | | 58 | Nigeria, Zaria, Zaria |
| 74-1 | E. barrelieri Daveau | | 60 | Macaronesia (Spain), Tenerife, Puerto de La Cruz |
| 75-94 | E. bicolor Nees | 10 | 20 | Ethiopia, Shoa (Shewa), Debra Zeit |
| 75-114 | !E. botryodes W.D. Clayton | | 80 | Ethiopia, Sidamo Borama, between Yavello and Aghera Mariam |
| 75-18 | E. capensis (Thunb.) Trin | | 40 | Zambia, Central Province, Lusaka |
| 75-167 | E. chapelieri (Kunth) Nees | | 20 | Mozambique, Maputo, Manhica |
| 75-152 | " | | 20 | Zambia, Central Province, Lusaka, Leopards' Hill |
| 75-139 | E. chloromelas Steud. | | ca 63 | + Hortus Botanicus, Coimbra, (Portugal) |
| 75-137 | E. cilianensis (All.) Lut. | | 20 | Portugal, Bira Litoral, Coimbra |
| 75-140 | " | | 20 | +Botanical Supply Unit, Egham, Surrey, England |

| | | | | |
|---|---|---|---|---|
| 78-5 | " | | 20 | France, Dordogne, Bergerac |
| 75-168 | " | | 40 | Mozambique, Maputo, Deane - Namaacha |
| 75-109 | " | | 60 | Ethiopia, Sidamo Borama, Negelli (Neghelli) |
| 75-169 | E. ciliaris (L.) R. Br. | | 20 | Mozambique, Maputo, Matola |
| 75-125 | " | | 20 | Uganda, Eastern Province, Serere |
| 75-145 | !E. congesta Oliv. | | 40 | Zimbabwe, Manicaland, Umtali, Uumba |
| 75-72 | E. curvula (Schard.) Nees | | 40 | +Botanischer Garten, Berlin -Dahlem, (Germany) |
| 75-73 | " | | 40 | +Botanischer Garten, Munchen - Nymphenburg,(Germany) |
| 75-95a | " | | 70 | Ethiopia, Shoa (Shewa), Debra Zeit |
| 75-78 | E. gangetica (Roxb.) Steud. | | 20 | Sierra Leone, Northern Province, Freetown |
| 75-64b | " | | 20 | Nigeria, Zaria, Zaria |
| 75-170 | E. heteromera Stapf | | 41 | Mozambique, Maputo, Namaacha |
| 75-107 | !E. kiwuensis Jedw. | | 40 | Ethiopia, Sidamo Borama, between Yirga - Alem and Negelli |
| 75-19 | E. lehmanniana Nees | | 40 | +Texas Plant Material centre, U.S.Depatment Of Agriculture |
| 75-70 | E. mexicana (Hornem.) Link. | 30 | 60 | +Hortus Botanicus Universitatis Osloensis, (Norway) |

| | | | | |
|---|---|---|---|---|
| 75-74 | " | | 60 | +Botanischer Garten, Berlin - Dahlem, (Germany) |
| 75-75 | E. minor Host | | 20 | +Botanischer Garten, Berlin -Dahlem, (Germany) |
| 75-134 | " | | 40 | France, Gard, Nimes |
| 75-88 | " | 20 | 40 | Botanical Garden of Armenian Academy of Sciences, Tashkent, (U.S.S.R.) |
| 75-69a | " | | 40 | Botanical Garden of Uzbek Academy of Sciences, Erevan, (U.S.S.R.) |
| 78-6 | " | | 40 | France, Dordogne, Bergerac |
| 78-7 | " | | 40 | France, Lot, Castelfranc |
| 75-65 | E. namaquensis Schrad. var. diplachnoides (Steud.) | | 20 | Nigeria, Zaria, Zaria |
| 75-161 | " | | 20 | Ghana, Northern Region, Mole Game Reserve |
| 78-9 | !E. orcuttiana Vasey | | 20 | France, Gironde, Hastignon St. Mèdard en Jalle |
| 75-113 | E. papposa (R.and S.) Steud. | | 40 | Ethiopia, Harar, Degahbur (Daghabur) |
| 75-147 | E. patens Oliv. | | 20 | Zimbabwe, Manicaland, Umtali, Uumba |
| 75-141 | E. pectinacea (Michx) Nees | | 40 | +Hortus Botanicus, Vacratot, (Hungary) |

| | | | | |
|---|---|---|---|---|
| 78-10 | " | | 60 | France, Gironde, La Haillau |
| 75-136 | E. pilosa (L.) P. Beauv. | 20 | 40 | Portugal, Beira Litoral, Montemor - o - Velho |
| 75-163 | " | | 40 | +Botanical Garden of Armenian Academy of Sciences, Erevan (U.S.S.R) |
| 75-95b | E. plana Nees | | 20 | Ethiopia, Shoa (Shewa), Debra Zeit |
| 75-130a | !E. porosa Nees | | 40 | Zimbabwe, Matabeleland, Matopos |
| 75-124 | E. racemosa (Thunb.) Steud. | | 20 | Uganda, Eastern Province, Serere |
| 75-130b | E. rigidior Pilg. | | 40 | Zimbabwe, Matabeleland, Matopos |
| 75-108 | !E. schwein-furthii Chiov. | | 40 | Ethiopia, Sidamo Borama, Kebra Mengist near Wadera |
| 75-85 | E. squamata (Lam.) Steud. | | 40 | Sierra Leone, Northern Province, Freetown |
| 75-173 | E. superba Peyr. | | 40 | Mozambique, Maputo, Namaacha |
| 75-128 | " | | 40 | Uganda, Eastern Province, Serere |
| 75-159 | " | | | Ghana, Eastern Region, Accra, Nurgua |
| 75-6 | E. tef (Zucc.) Trotter | | 40 | +Ethiopia, Shoa (Shewa), Debra Zeit |
| 75-7 | " | 20 | 40 | +Ethiopia, Shoa (Shewa), Debra Zeit |
| 75-9 | " | | 40 | +Ethiopia, Shoa (Shewa), Debra Zeit |

| | | | | |
|---|---|---|---|---|
| 75-12 | " | 20 | 40 | †Ethiopia, Shoa (Shewa) Debra Zeit |
| 75-14 | " | | 40 | †Ethiopia, Shoa (Shewa), Debra Zeit |
| 75-93 | " | 20 | 40 | †Ethiopia, Shoa (Shewa), Debra Zeit |
| 75-117 | " | | 40 | †Ethiopia, Shoa (Shewa), Debra Zeit |
| 75-80 | E. tenella (L.) P. Beauv. | | 20 | Sierra Leone, Northern Province, Freetown |
| 75-105 | E. tenuifolia (A. Rich.) Steud. | | 41 | Ethiopia, Sidamo Borama, between Yavello and Aghera Mariam |
| 75-98 | " | | 40 | Ethiopia, Sidamo Borama, Lake Awasa |
| 75-100 | " | | 40 | Ethiopia, Sidamo Borama, between Yirga - Alem and Negelli |
| 75-119 | " | | 40 | Ethiopia, Shoa (Shewa), east of Lake Awasa |
| 75-115 | " | | 40 | Zambia, Northern Province, Makulu Mont. |
| 75-20 | E. trichodes (Nutt.) Wood. | | 40 | +Kansas Plant Material Centre, U.S. Department of Agriculture |
| 75-21 | " | | 40 | Nebraska, Miller Co., U.S. Department of Agriculture |
| 75-22 | " | | 40 | Texas Plant Material Centre, U.S. Department of Agriculture |

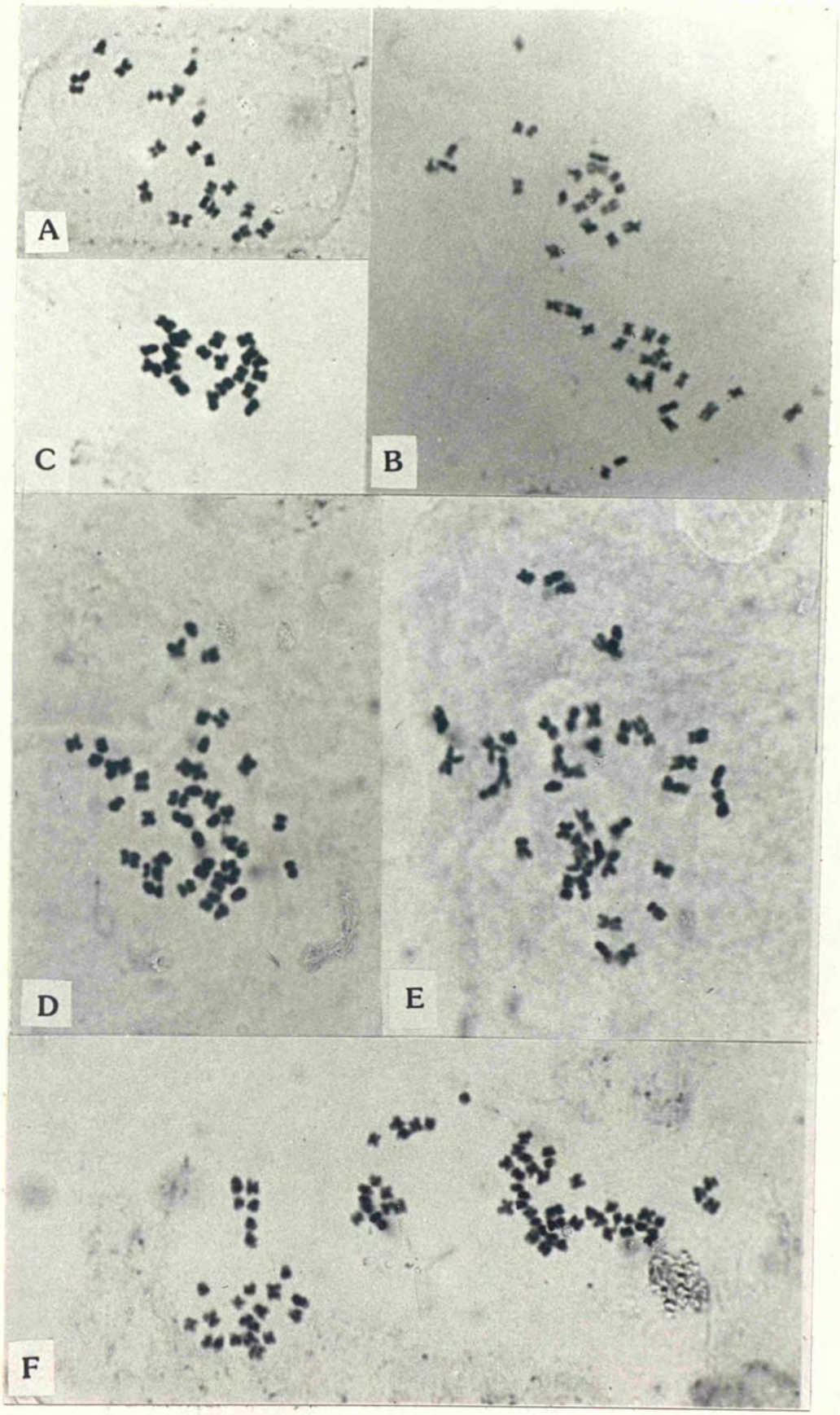
| | | | | |
|---|---|---|---|---|
| 75-83 | E. unioloides (Retz.) Nees | | 20 | Sierra Leone, Northern Province, Freetown |

! First chromosome counts for this species

\+ Seeds of unknown origin grown (eg. at a Botanical Garden

PLATE 2.1 Somatic chromosomes of some Eragrostis species whose chromosome number was previously unknown. (Root-tip mitoses pretreated with colchicine, all X 2200).

| | | | |
|---|---|---|---|
| A. | E. aethiopica | 75- 1 | 2n = 20 |
| B. | E. congesta | 75-145 | 2n = 40 |
| C. | E. orcuttiana | 78- 9 | 2n = 20 |
| D. | E. porosa | 75-130a | 2n = 40 |
| E. | E. schweinfurthii | 75-108 | 2n = 40 |
| F. | E. botryodes | 75-114 | 2n = 80 |


A
B
C
D
E
F

New chromosome numbers, differing from the numbers previously reported, were obtained for seven other Eragrostis species (see Table 2.2). These new counts are: 2n=60 for E. cilianensis, 2n=70 for E. curvula, 2n=40 for E. papposa, 2n=20 for E. racemosa, 2n=58 for E. atrovirens, 2n=41 for E. heteromera and 2n=41 for E. tenuifolia. Mitotic preparations of some of these species are shown in Plate 2.2.

Chromosome numbers for twenty-six Eragrostis species confirmed the previously published counts for these species. Plates 2.3 to 2.9 show some of these mitoses.

Chromosome numbers of all Eragrostis species studied by the present author were multiples of 10, except for E. chloromelas with 2n=ca.63, E. atrovirens with 2n=58, E. heteromera with 2n=41 and one accession of E. tenuifolia (75-115) with 2n=41. These are illustrated in Plate 2.10.

A comprehensive list was made of all chromosome counts for Eragrostis species, including previously published chromosome counts and the counts made by the present author; these are given in Appendix 1. The chromosome counts reported by Leigh (1980), which are all "circa" are given in Appendix 2; for this reason they are not included in my discussions.

Table 2.2 New Chromosome numbers for Eragrostis species whose numbers have been previously reported

| Species | New count | Previous counts |
|---|---|---|
| E. atrovirens (Desf.) Steud. | 58 | 40, 60 |
| E. cilianensis (All.) Lut. | 60 | 20, 40, 70 |
| E. curvula (Schrad.) Nees | 70 | 20, 40, 50, 60, 80, 42, 63 |
| E. heteromera Stapf. | 41 | 40 |
| E. papposa (R. and S.) Steud. | 40 | 20 |
| E. racemosa (Thunb.) Steud. | 20 | 40, 60, 62 |
| E. tenuifolia (A.Rich.) Steud. | 41 | 40 |

See Appendix 1 for details of provenance of material and for details of previous counts.

PLATE 2.2 Somatic chromosomes of some Eragrostis species for which new chromosome numbers have been obtained (former counts in parentheses). (Root-tip mitoses pretreated with colchicine, all X 2200).

A. E. atrovirens, 75-61 2n = 58 (20,40,60)

B. E. curvula, 75-95a 2n = 70 (20,40,42,50,60,63,80)

C. E. heteromera, 75-170 2n = 41 (40)

D. E. tenuifolia, 75-115 2n = 41 (40)

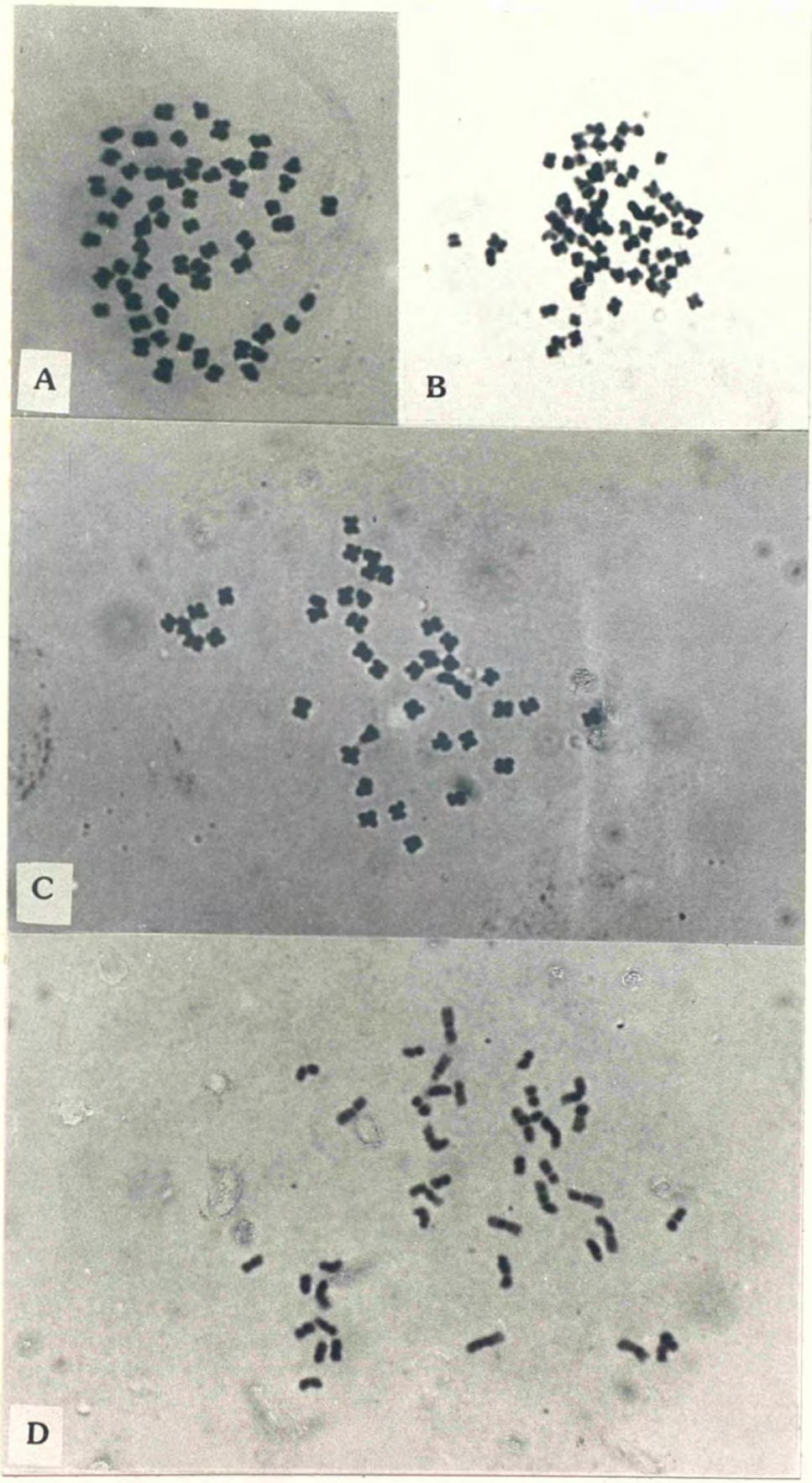

A
B
C
D

PLATE 2.3 Somatic chromosomes of some Eragrostis species confirming reported diploid counts of 2n = 20. (Root-tip mitoses pretreated with colchicine, all X 2200).

A. E. aspera 75-144

B. E. bicolor 75- 94

C. E. cilianensis 75-140

D. E. ciliaris 75-169

E. E. gangetica 75- 78

F. E. plana 75-95b

(See also Plate 2.4)

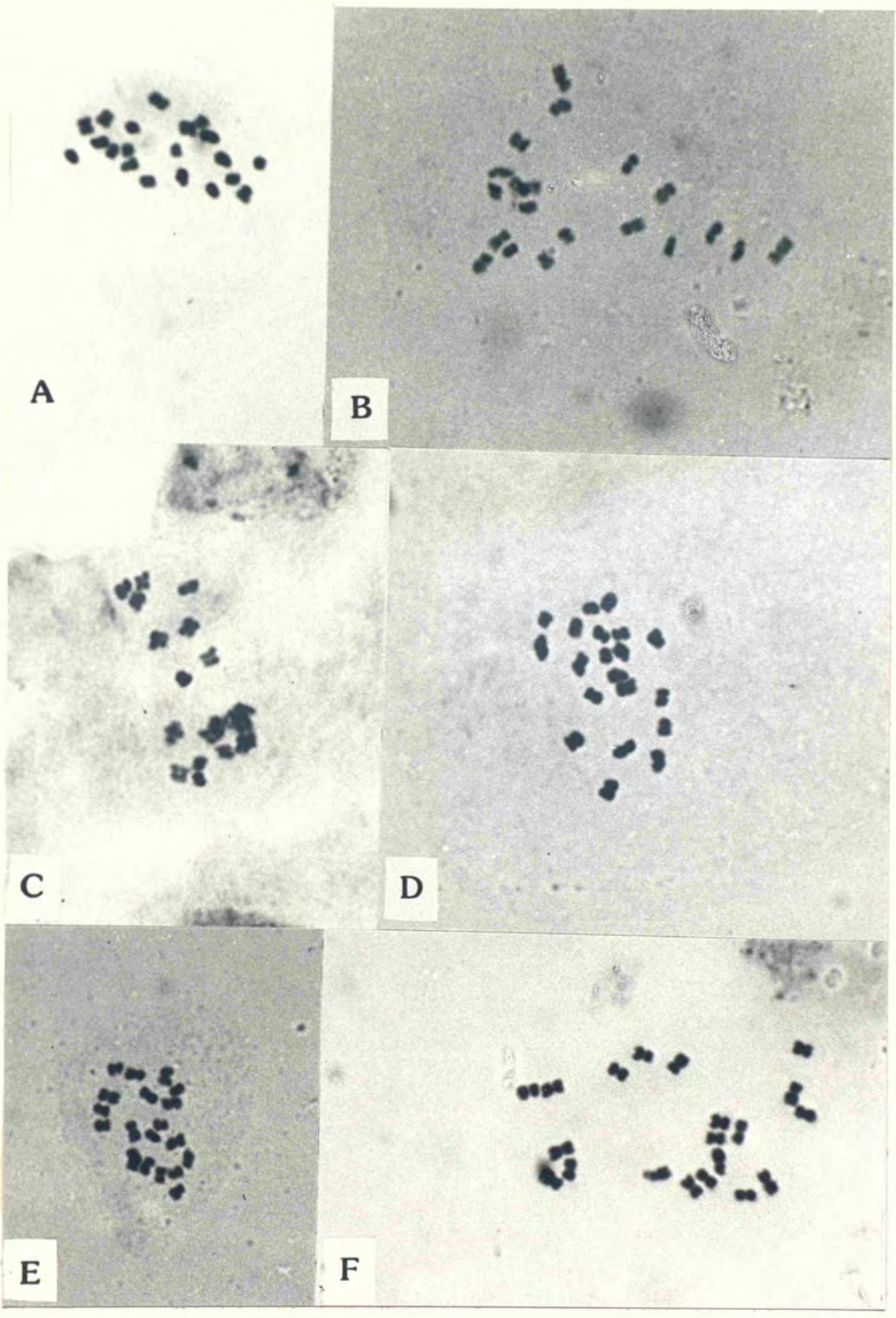

A
B
C
D
E
F

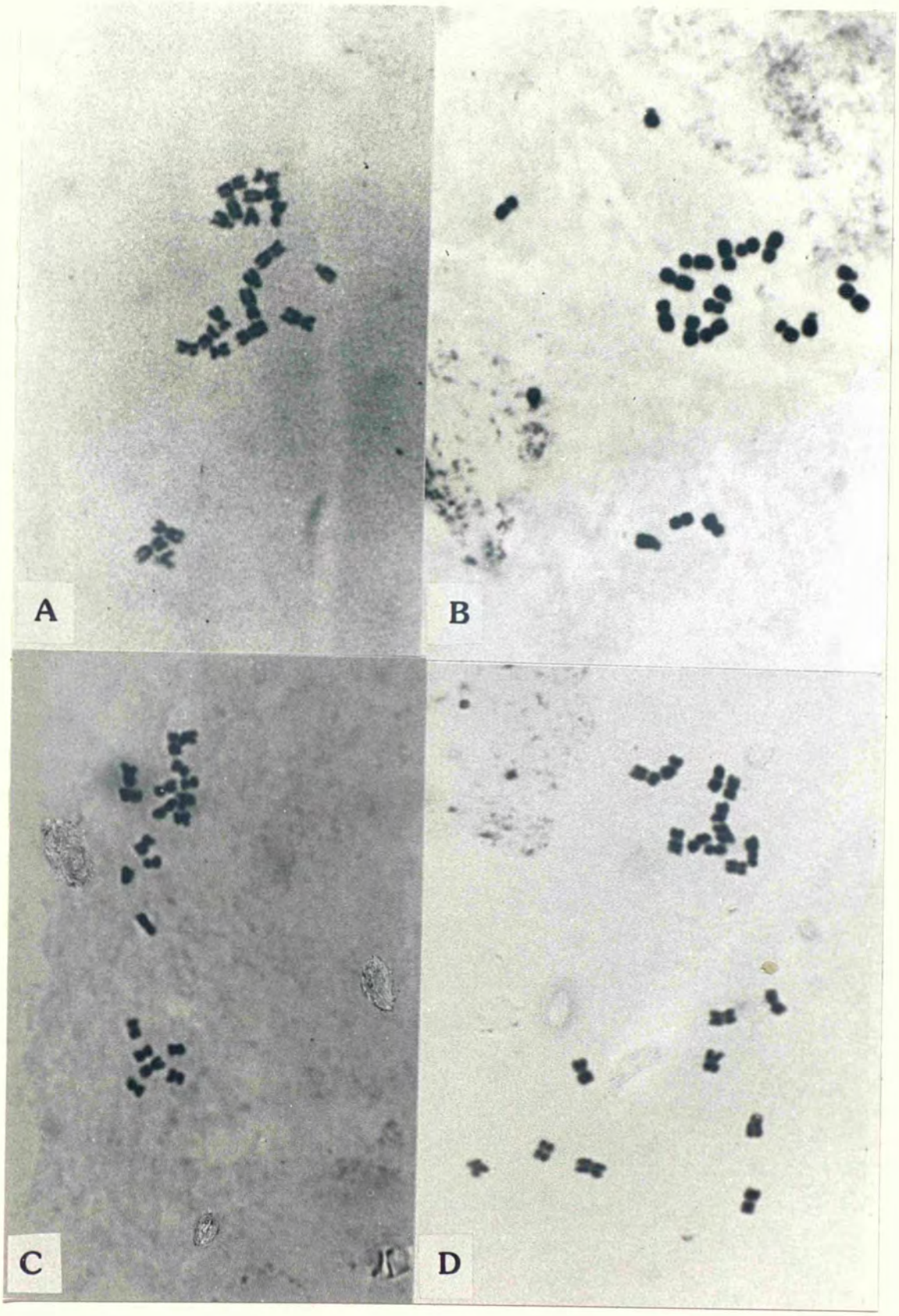
PLATE 2.4 Somatic chromosomes of some Eragrostis species confirming reported diploid counts of 2n = 20. (Root-tip mitoses pretreated with colchicine, all X 2200 ).

A. E. namaquensis var. diplachnoides 75-65

B. E. " " " 75-161

C. E. patens 75-147

D. E. racemosa 75-124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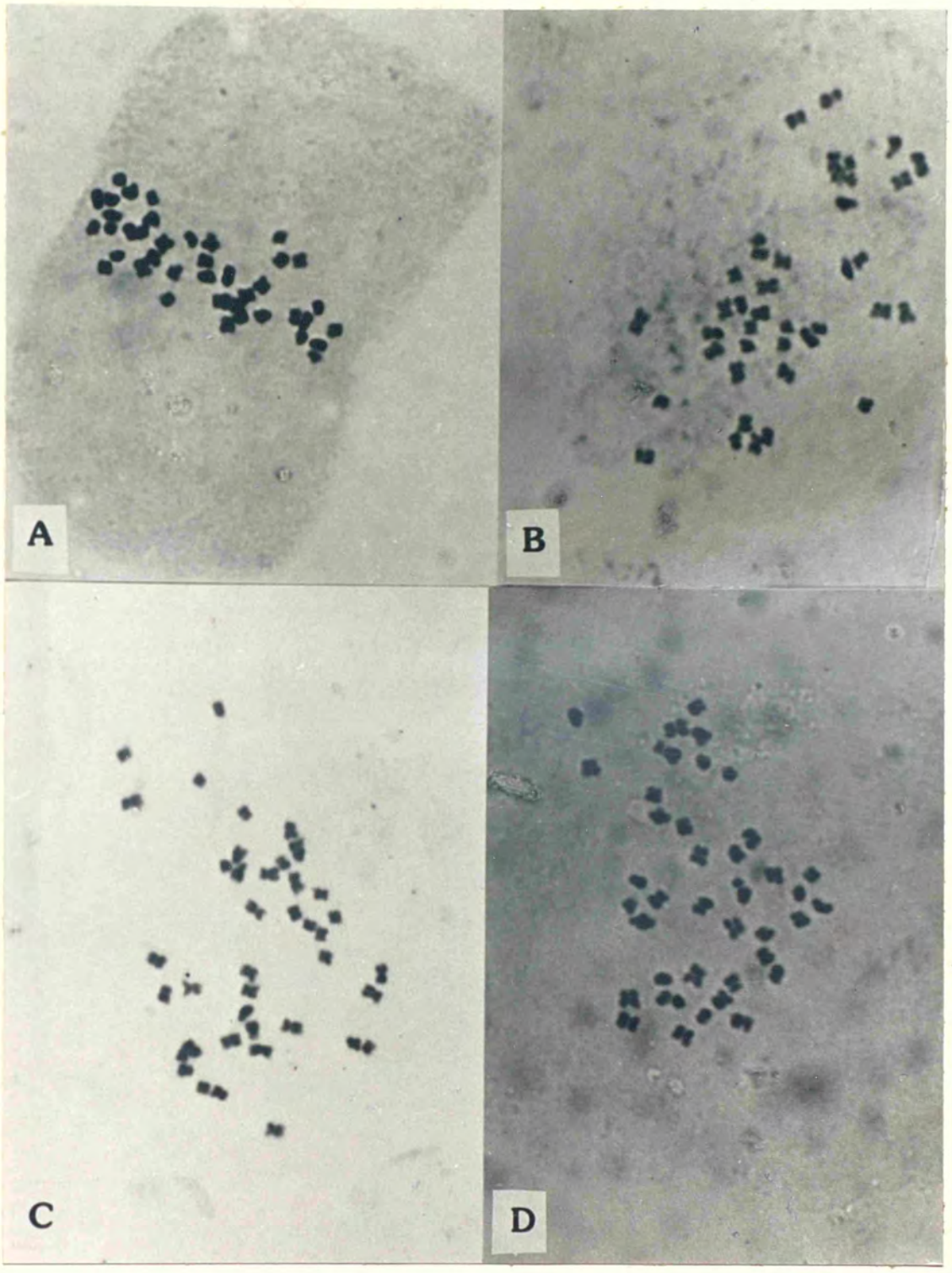



PLATE 2.5 Somatic chromosomes of some Eragrostis species confirming reported tetraploid counts of 2n = 40.

(Root-tip mitoses pretreated with colchicine, all X 2200.

A. E. tef 75-12 B. E. tef 75-6

C. E. tef 75-7 D. E. pilosa 75-163

(see also Plate 2.6 to 2.8).

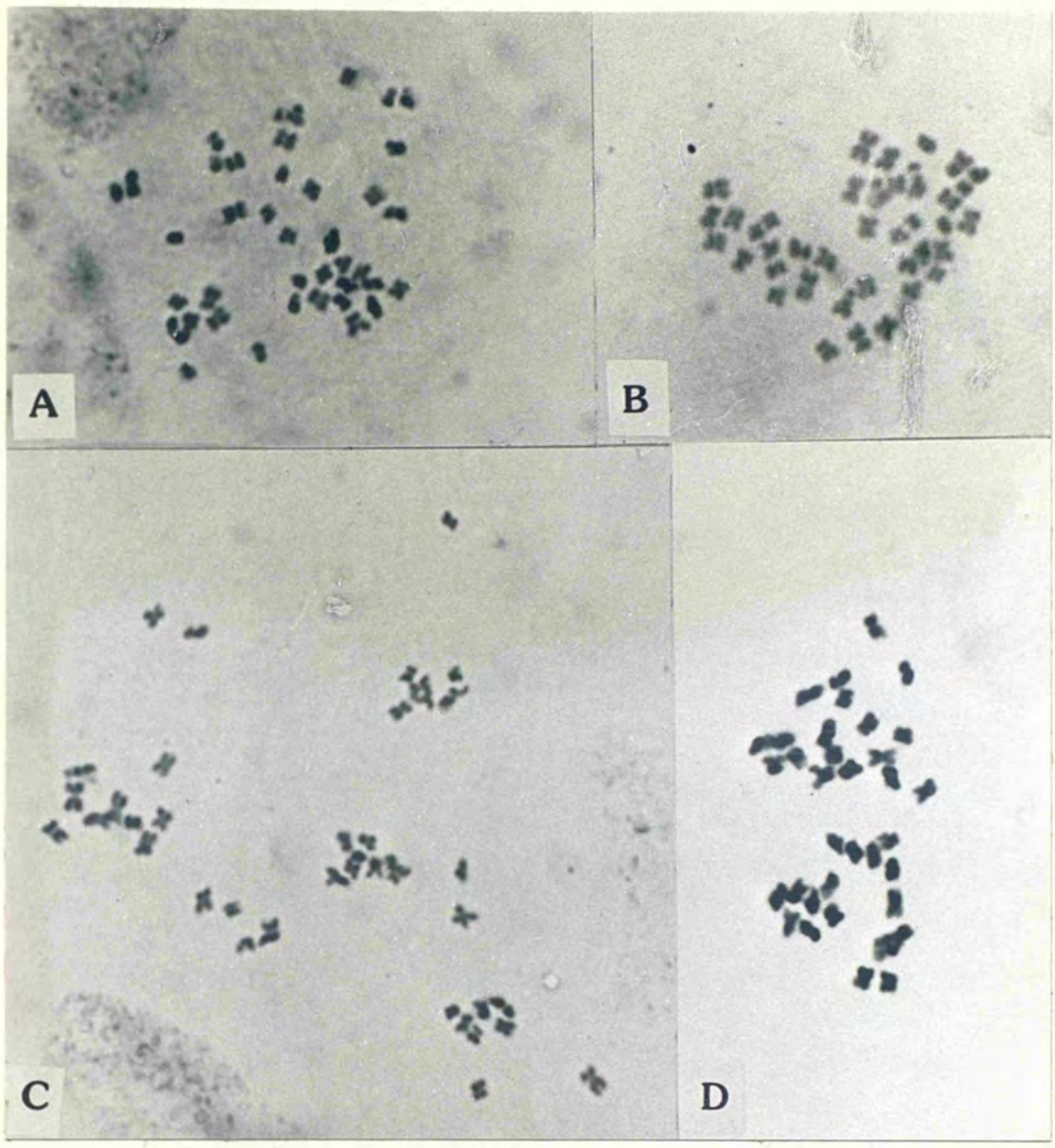



PLATE 2.6 Somatic chromosomes of some Eragrostis species confirming reported tetraploid counts of 2n = 40. (Root-tip mitoses pretreated with colchicine, all X 2200).

A. E. pilosa 75-136

B. E. minor 75-134

C. E. minor 75- 88

D. E. rigidior 75-130

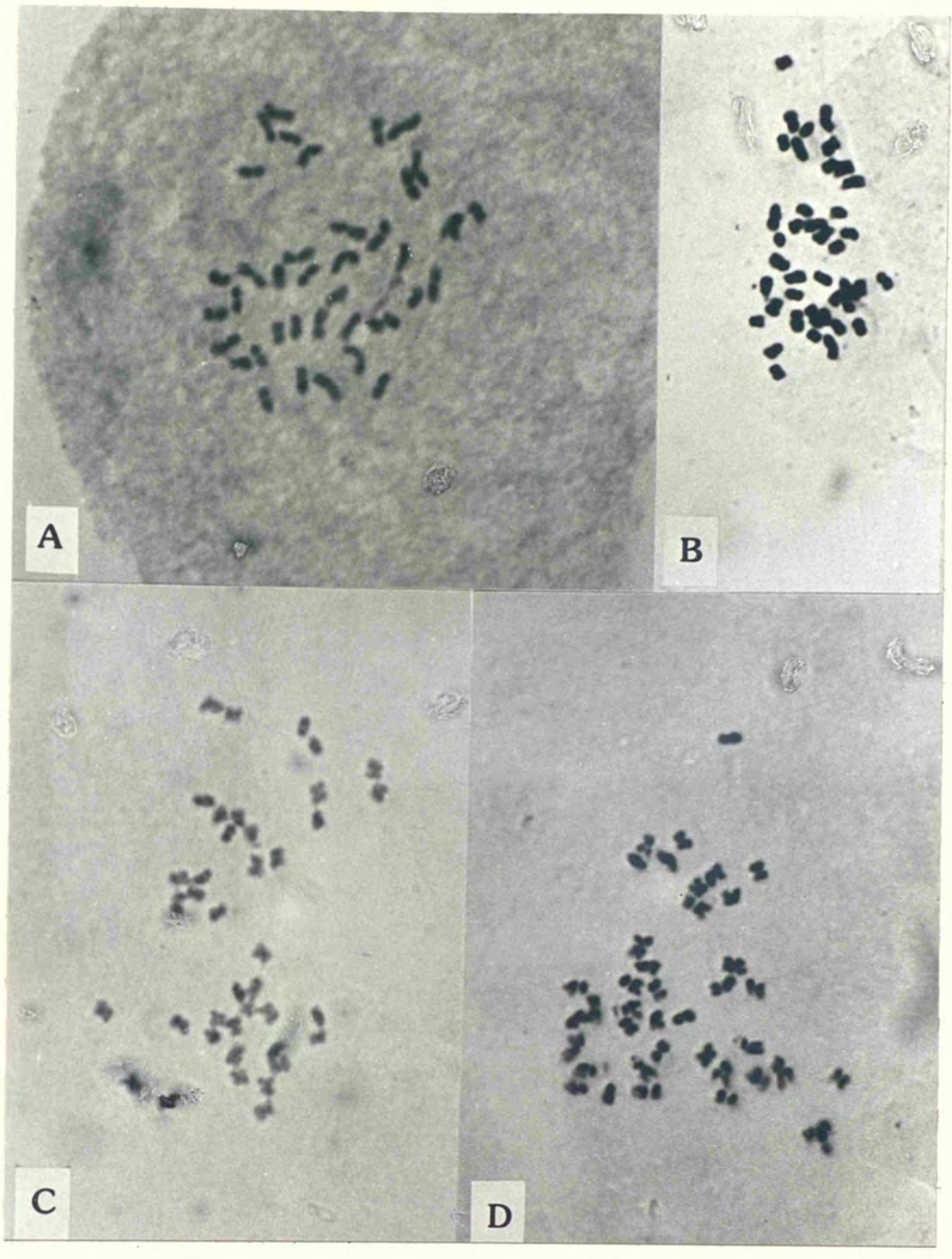



PLATE 2.7 Somatic chromosomes of some Eragrostis species confirming reported tetraploid counts of 2n = 40.

(Root-tip mitoses pretreated with colchicine, all X 2200).

A. E. cilianensis 75-168

B E. tenuifolia 75-126

C. E. lehmanniana 75- 19

D. E. trichodes 75- 22

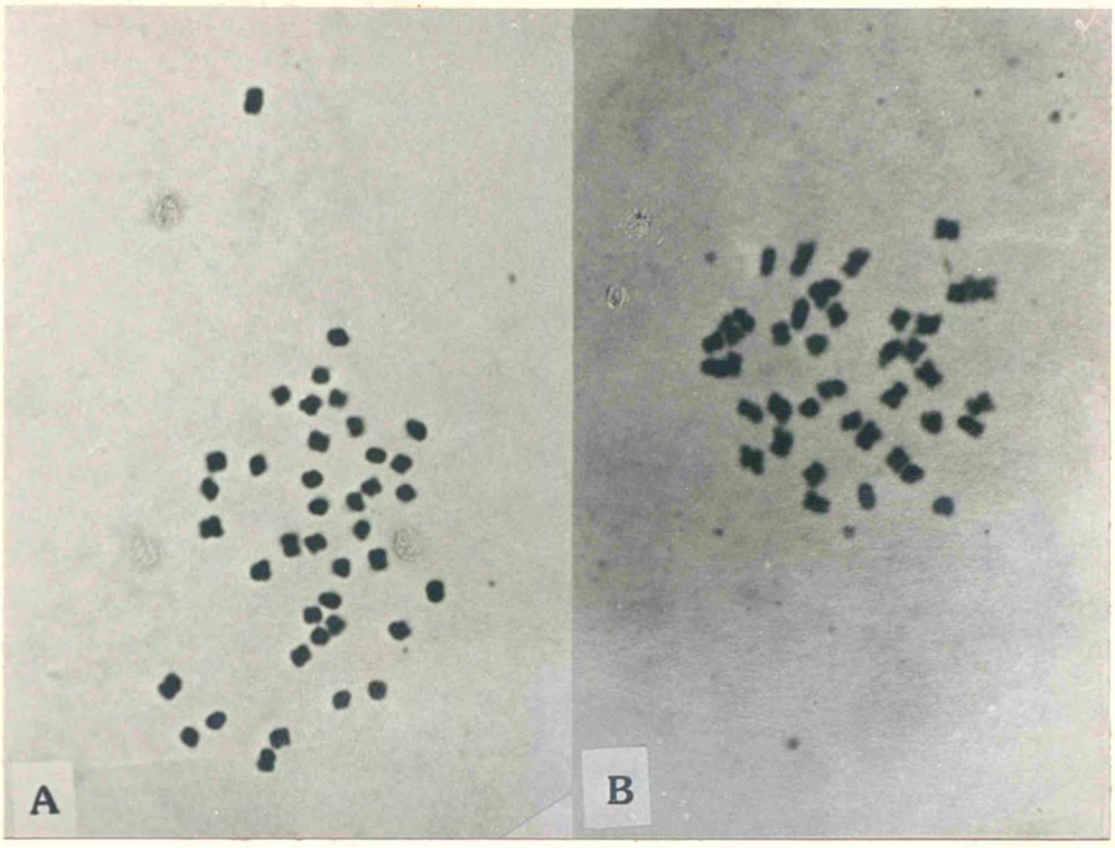



PLATE 2.8 Somatic chromosomes of some Eragrostis species confirming reported tetraploid counts of 2n = 40. (Root-tip mitoses pretreated with colchicine, all X 2200).

A. E. superba 75-128.

B. E. chapelieri 75-152.

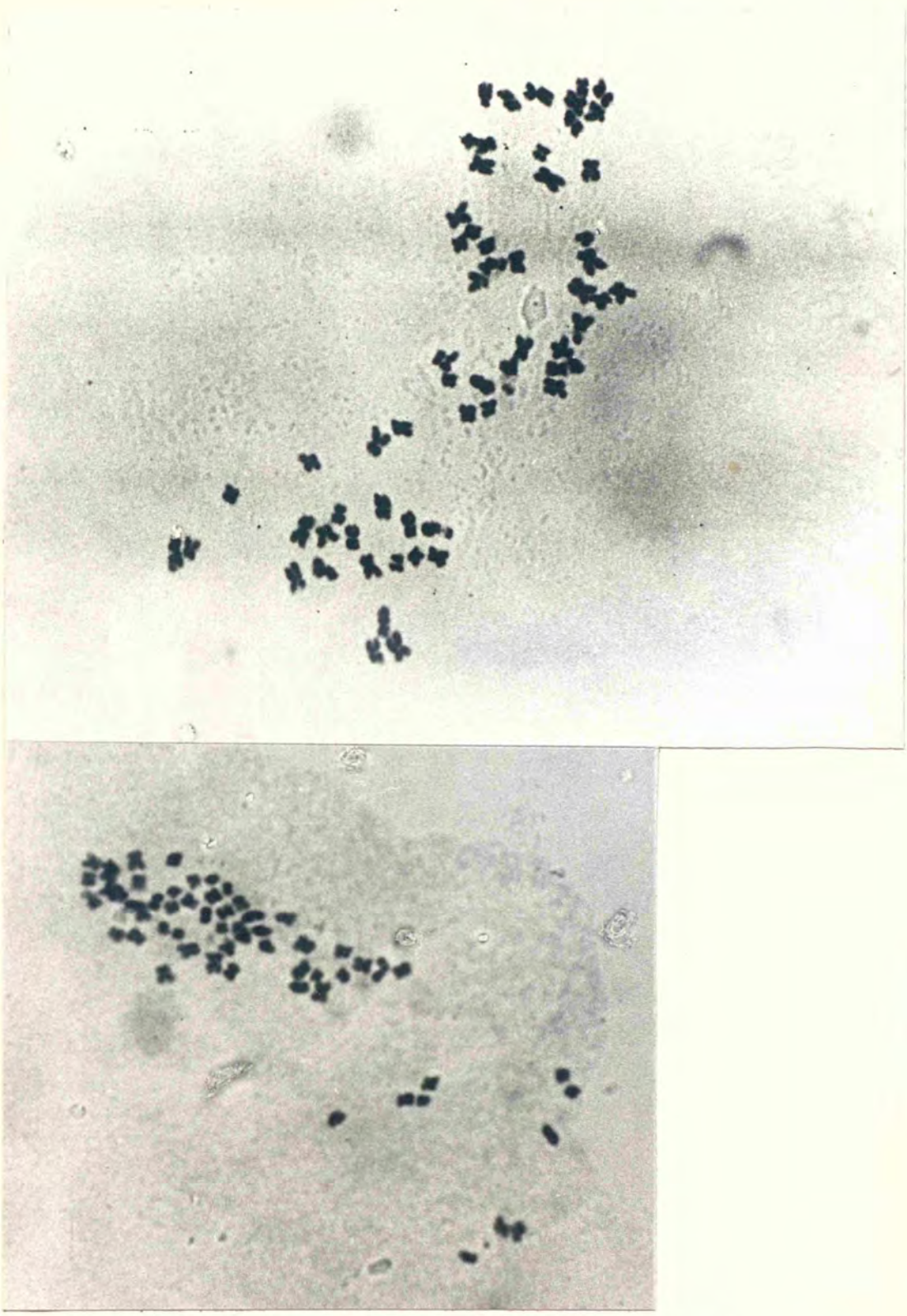


PLATE 2.9 Somatic chromosomes of two accessions of *E. mexicana* confirming hexaploid counts of 2n = 60. (Root-tip mitoses pretreated with colchicine, all X 2200).

Top: *E. mexicana* 75-70.

Bottom: *E. mexicana* 75-74.

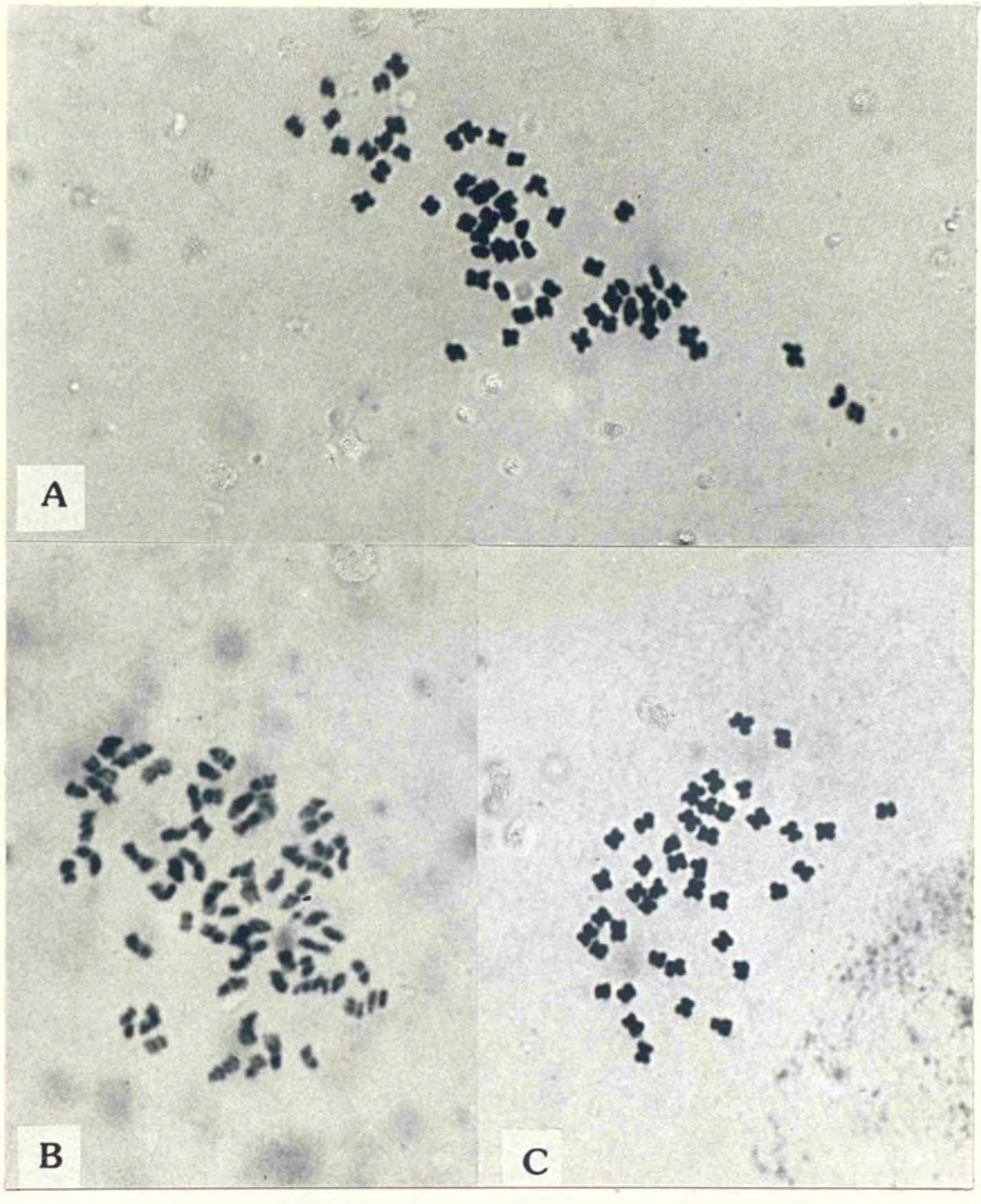



PLATE 2.10 Somatic chromosomes of aneuploid plants of three Eragrostis species. (Root-tip mitoses pretreated with colchicine, all X 2200).

A. E. atrovirens 75- 61 2n =58 (see also plate 2.2A).

B. E. chloromelas 75-139 2n =Ca.63.

C. E. heteromera 75-170 2n =41 (see also plate 2.2C).

(Somatic chromosomes of aneuploid plant of E. tenuifolia was previously illustrated as plate 2.2D 2n = 41).

The somatic chromosome numbers determined for Eragrostis by the writer range from 20 to 80 (Table 2.1); the published counts range from 18 to 120 (Appendix 1). Most of these counts are multiples of ten; only 24 counts are reported which are not multiples of ten, four of them by the present author.

Data extracted from Appendix 1 are given in Table 2.3; it shows that the majority (85 out of 120 species) have only one reported level of polyploidy. The most numerous category are the tetraploids; there are twice as many of them as of the next most numerous class, the diploids. Hexaploids are relatively numerous: they are about one-sixth of the total. Higher polyploids are less common and odd polyploids are rarer still. Seven of the species have chromosome numbers which are not multiples of ten; four of these also have counts, differing only by one chromosome, which are multiples of ten; three of them have counts which are the only ones reported for these species.

Thirty-five species (out of 120) have more than one level of 'ploidy (Table 2.4). Few of the species which have been extensively studied have only one chromosome number reported. Notable among these are: E. barrelieri (2n=60), E. trichodes (2n=40), E. chapelieri (2n=20) all of which have also been examined by me. Most well-studied species have two or

Table 2.3 Number of Eragrostis species with only one level of 'ploidy reported

| Somatic chromosome number | Number of species |
|---|---|
| 20 | 21 |
| 30 | 1 |
| 40 | 40 * |
| 50 | 1 |
| 60 | 13 |
| 70 | 2 ** |
| 80 | 5 *** |
| 100 | 2 |
| Total | 85 |

* Includes four species with counts of both 2n=40 and 41 and one species with 2n=44.

** Includes one species with 2n=72.

*** Includes one species with 2n=84.

Table 2.4 Number of Eragrostis species with various combinations of 'ploidy levels

| Somatic chromosome number | Number of species |
|---|---|
| 20, 40 | 10 |
| 20, 30, 40 | 2 |
| 20, 30, 40, 60 | 1 |
| 20, 40, 50, 60 | 1 |
| 20, 40, 50, 60, 70, 80 | 1 |
| 20, 40, 60 | 5 |
| 20, 40, 60, 70 | 1 |
| 20, 40, 80 | 1 |
| 30, 40 | 1 |
| 40, 50, 60 | 1 |
| 40, 60 | 4 |
| 40, 60, 80 | 2 |
| 40, 60, 70*, 80 100, 110*, 120 | 1 |
| 40, 80 | 1 |
| 60, 80 | 1 |
| 60, 90 | 1 |
| 70, 80 | 1 |
| Total | 35 |

* Aneuploid counts of 2n=72, 74 and 108 are included here.

more chromosome races. Particularly notable among these are: E. cilianensis (2n=20*, 40*, 60*, 70), E. curvula (2n=20, 40*, 50, 60, 70*, 80, also 42 and 63), E. intermedia (2n=40, 60, 80, 100, 120, also 72, 74, 76, 108), E. minor (2n=20*, 30, 40*, 60, also 44), E. pilosa (2n=20, 40*, 50, 60).

Chromosome numbers which are not integral multiples of ten have been reported in seventeen species. Three of these species have two or more such counts: E. curvula (2n=42, 63), E. chloromelas (2n=61, 62, 63) and E. intermedia (2n=72, 74, 76, 108). Three species (out of the seventeen) have only one reported count: E. airoides (2n=72), E. grandis (2n=44), and E. swaleni (2n=84). The other fourteen species are remarkable in having aneuploid and euploid chromosome numbers with euploid counts predominant. As mentioned earlier, I have observed aneuploid chromosome numbers in four species: E. atrovirens (2n=58), E. chloromelas (2n=ca.63), E. heteromera (2n=41) and E. tenuifolia (2n=41) (Plate 2.2 and 2.10).

2.3.2 Meiosis

Meiotic behaviour of three accessions of E. tef

*I have contributed or confirmed the asterisked numbers.

(75-7, 75-12 and 75-93) and of five species considered to be related to E. tef (Jones, Ponti, Tavassoli and Dixon, 1978) were studied. These include three annual species: E. aethiopica, E. pilosa, E. mexicana and two perennial species: E. bicolor and E. heteromera.

Meiosis was normal in all three accessions of E. tef. Twenty bivalents were observed at diakinesis and at metaphase I in ten pollen mother cells (P.M.C.) of accession 75-7, in twenty-eight P.M.C.'s of accession 75-12 and in eighteen P.M.C.'s of accession 75-93 (Plate 2.11). Anaphase I was also normal in all the three accessions of E. tef. These are the first observations of meiosis in this Ethiopian cereal.

Meiosis was also normal in the three other annual species studied. Ten bivalents were observed at diakinesis and metaphase I in twenty P.M.C.'s of E. aethiopica; twenty bivalents were observed in fourteen P.M.C.'s of E. pilosa and thirty bivalents were observed in thirty pollen mother cells of E. mexicana (Plate 2.11). Anaphase I was also normal in all the three species. In E. pilosa, very occasionally one or two chromosomes did not line up with the others on the plate of metaphase I (Plate 2.11).

PLATE 2.11 Meioses of Eragrostis tef and three related species.

A. E. aethiopica 75-1 metaphase I with 10 bivalent X 1100.

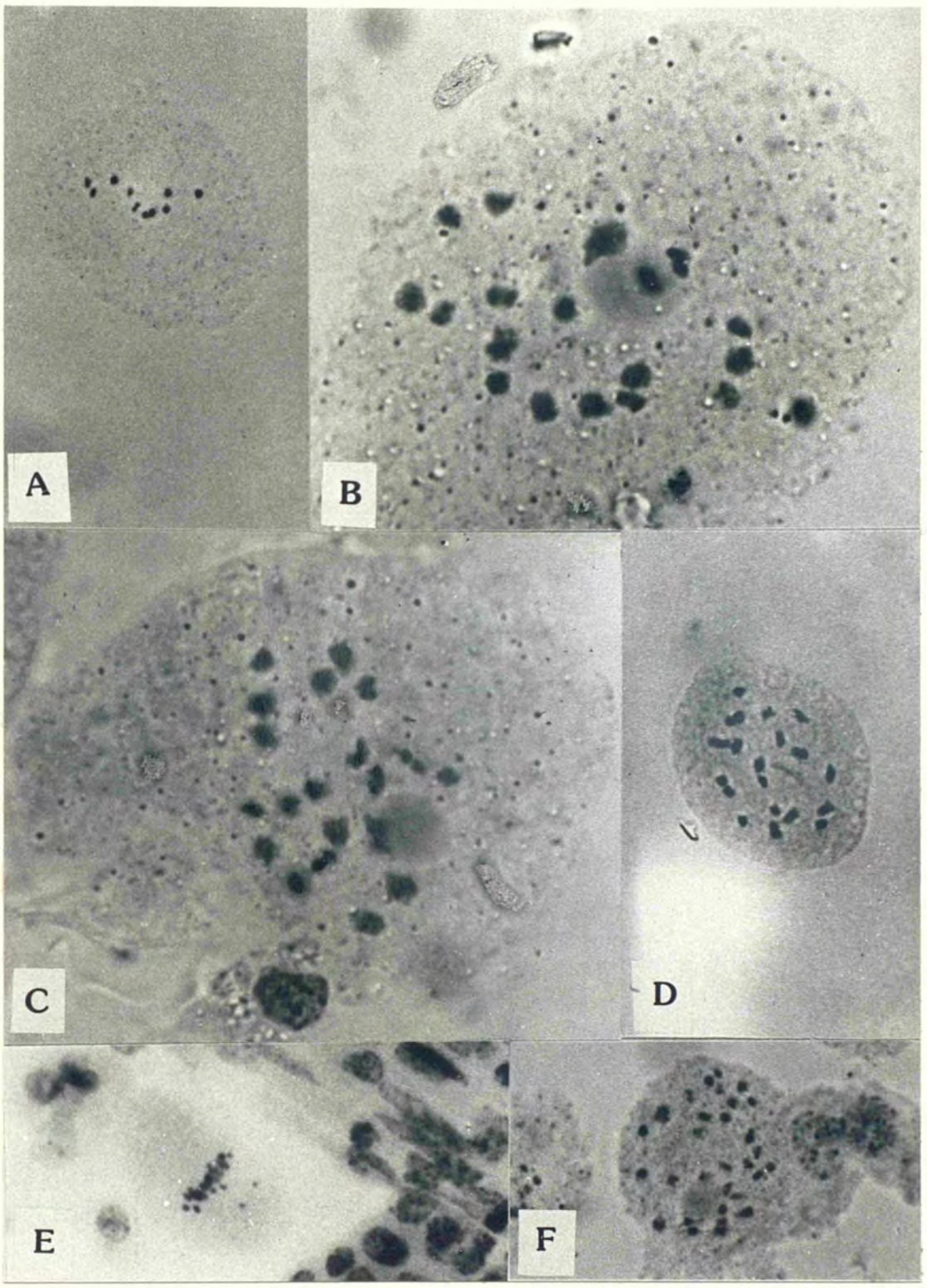
B. E. tef 75-12 diakinesis with 20 bivalents X 2200.

C. E. tef 75-7 diakinesis with 20 bivalents X 2200.

D. E. pilosa 75-136 late diakinesis with 20 bivalents X 1100.

E. E. pilosa 75-136 metaphase I showing two univalents which are not on the equatorial plate X 1100.

F. E. mexicana 75-70 diakinesis with 30 bivalents X 1100.


A
B
C
D
E
F

Among the two perennial species closely related to E. tef, E. bicolor had regular meiosis with ten bivalents at metaphase I, but the studied plants of E. heteromera, with a somatic chromosome number of 2n=41, had irregular meiosis (Plate 2.12). The bivalents showed strong secondary association and in some cells one quadrivalent was seen. In other cells no multivalent was observed. A single unpaired chromosome was recognisable in many cells. This univalent was particularly obvious after first division, being often separate from the plate of metaphase II, appearing as a late-dividing laggard at second anaphase. Micronuclei, which may incorporate such laggard chromosomes, were observed in some tetrads.

Among the plants which were raised, one accession (75-69) of E. minor was observed to include completely sterile plants and no seed was formed. Another accession of E. minor (75-88) was partially sterile. This accession formed very few seeds during the winter, but produced more during spring, becoming fertile during the summer. Meiotic behaviour of these two accessions (75-88 and 75-69) of E. minor was studied. In the completely sterile plant of E. minor (75-69), meiosis was irregular (Plate 2.13). In twenty-one pollen mother cells at diakinesis roughly equal number of bivalents and univalents were observed (13II and 14I). Between three to ten laggards were observed at anaphase I. (See p.127)

PLATE 2.12 Meiosis in aneuploid Eragrostis heteromera with 2n = 41.

A. Diakinesis with 18 bivalents (some showing secondary association, one quadrivalent and one univalent X 2200.

B. Late anaphase I showing laggard univalent X 2200.

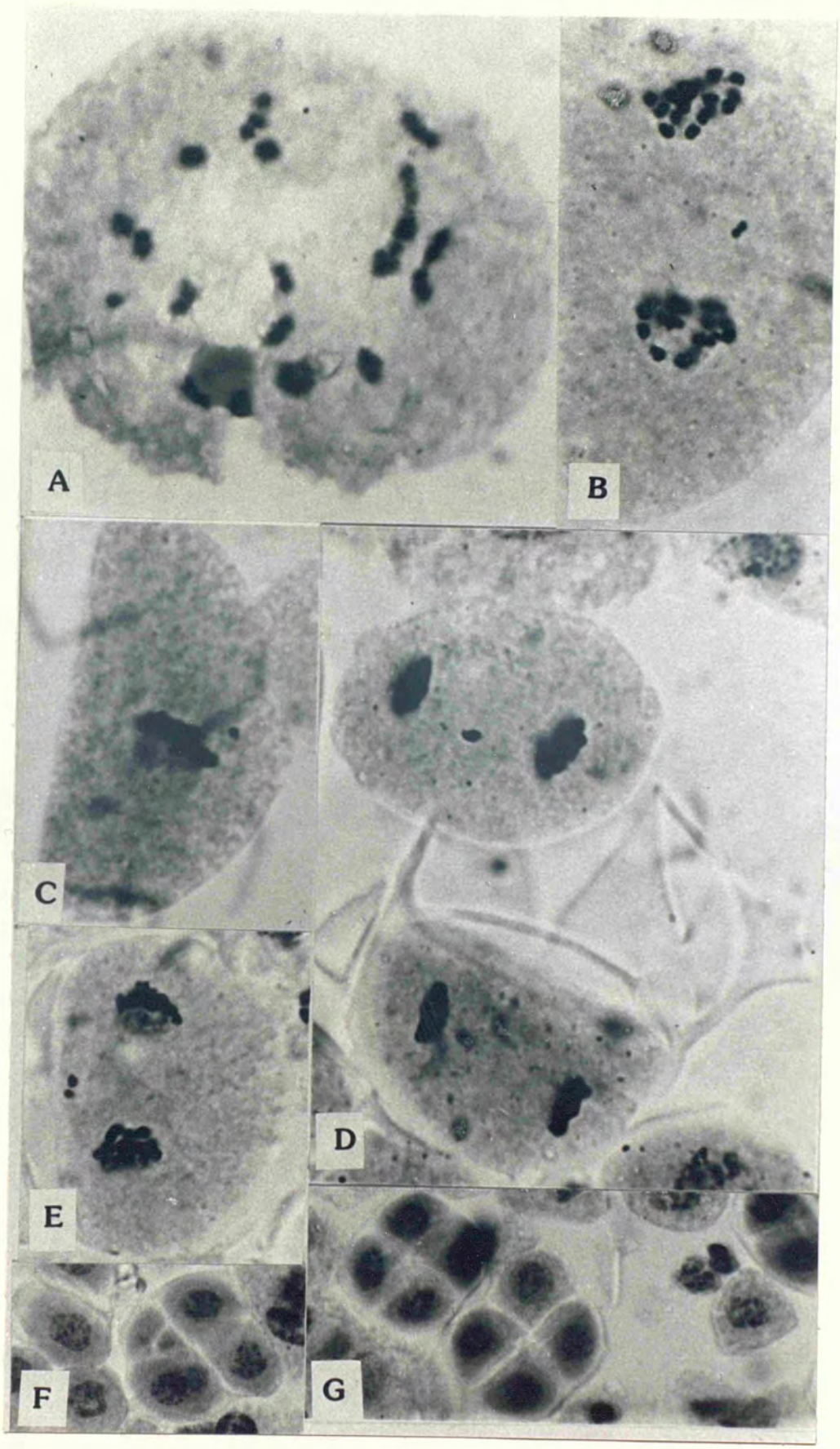
C. Metaphase II with attendant univalent X 2200.

D. Telophase II: one daughter cell has a still-undivided extra chromosome X 2200.

E. Late anaphase II showing the late-dividing extra chromosome X 2200.

F. Tetrad with micronuclei X 1000.

G. Normal tetrad for comparison X 1000.


A
B
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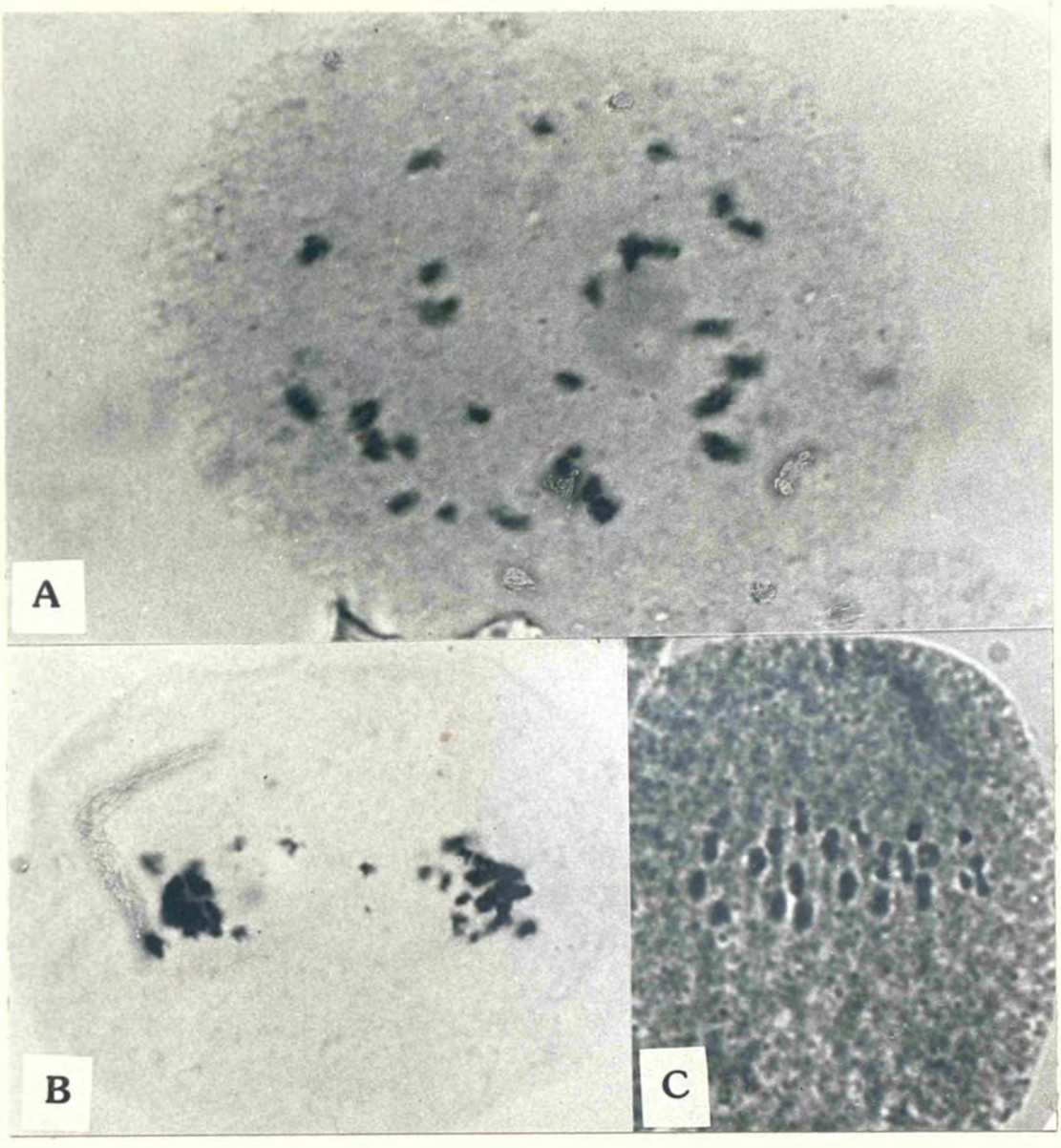



PLATE 2.13 Meioses of sterile plants of Eragrostis minor (2n=40).

A. Diakinesis of the permanently sterile 75-69, with roughly equal numbers of bivalents and univalents X 2200.

B. Anaphase I of 75-69, showing laggards X 2200.

C. Metaphase I of 75-88, showing 20 bivalents in this winter-sterile race X 2200.

Meiosis in the less sterile plant of E. minor (75-88) was normal with twenty bivalents at metaphase I (Plate 2.13). Anaphase was also normal in this accession.

## 2.4 Discussion

### 2.4.1 Cytology of the genus

Eragrostis is a large genus (c. 300spp.) whose species are mainly confined to the arid and semiarid warm regions of the world. Although tropical genera are generally cytologically less well studied than their temperate counterparts, Eragrostis with reported chromosome counts for 120 species (Appendix 1) is one of the better known genera. This allows us to arrive with some confidence at conclusions about base number, the frequency of polyploidy and aneuploidy in the genus.

### 2.4.2 Base number of the genus

The lowest reported somatic chromosome number in an Eragrostis species is twenty, apart from a single count of eighteen for one race of E. unioloides (Mehra and Sharma, 1975). The count of 2n=20 has been found in forty-three species, including E. unioloides itself (Appendix 1). The euploid chromosome numbers in the

genus fell into a regular pattern of frequency categories with even multiples of ten being much more numerous than odd multiples (Fig.2.1). For these reasons, it seems likely that the base number of the genus is ten (x=10). Eight, nine and ten are reported as the base numbers for the tribe Eragrosteae (Gould, 1968). Ten has been assumed to be the base number of the genus Eragrostis by most previous authors (Pienaar, 1953; de Wet, 1954; Darlington and Wylie, 1955; Gould, 1968b; Busey, 1976; Tsvelev, 1976).

However, Roy (1965) has suggested the possibility of five being the primary base number for Eragrostis. He found that in E. diarrhena, with gametic chromosome number of n=10, in 18% of pollen mother cells all the chromosomes were secondary associated as five groups, each group composed of two bivalents. He commented that these groups might easily be mistaken for quadrivalents, and indeed his Fig.2 shows three chromosome groups which look more like quadrivalents than secondarily associated bivalents. These secondary associations (or quadrivalents) seem to indicate homology between four chromosomes in this "diploid" species. Unfortunately no other authors have reported any comparable phenomenon to support Roy's suggestion. My observation of secondary association indicates that not all the chromosomes were involved in the tetraploid (2n=41) of E. heteromera which alone showed this phenomenon. The other six

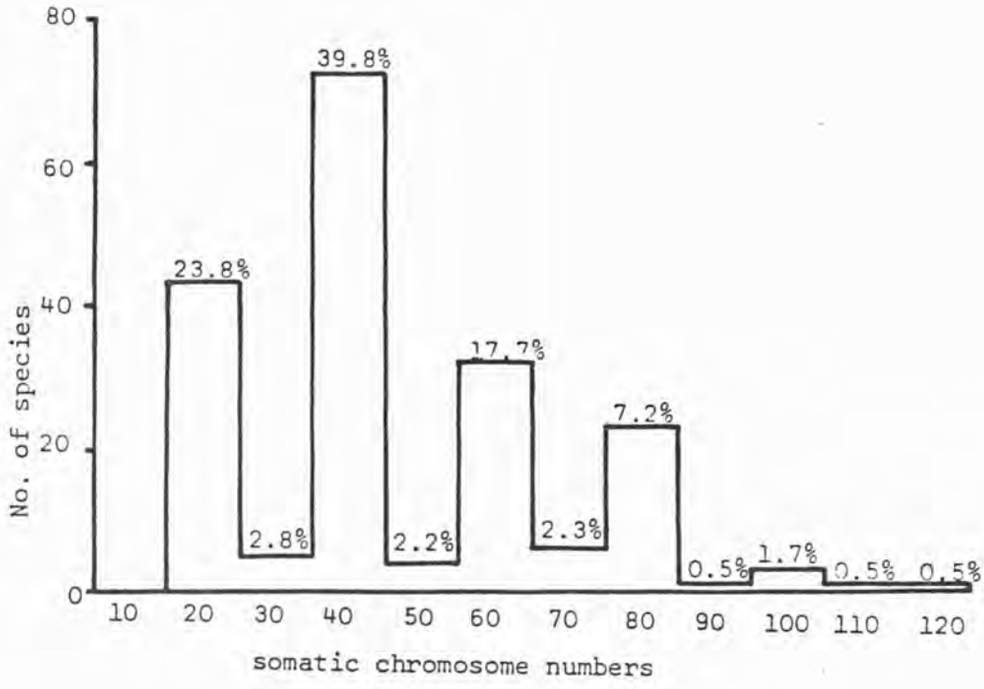



Fig. 2.1 Frequency of chromosome races in species of Eragrostis.

Aneuploid counts are included in the nearest euploid number.

species studied meiotically, which included diploid, tetraploid and hexaploid species of Eragrostis, showed neither multivalent nor secondary association.

The count of 2n=18 for E. unioloides by Mehra and Sharma (1975) could be interpreted as the stabilised result of chromosome loss from a tetraploid (2n=20) condition, since chromosome loss may be fatal to a diploid, while in a polyploid, the unbalance may be too little to cause trouble (Darlington, 1973). However it could equally be explained as a case of Robertsonian translocation in a diploid (cf. Gibasis: Jones, 1974). It is worth noting that Mehra and Sharma (1975), reported that meiosis in E. unioloides was quite normal with nearly 100% pollen fertility.

Among the one hundred and twenty Eragrostis species whose chromosome numbers have been reported (Appendix 1), no less than thirteen species have at least one count reported which is an odd multiple of ten. The only known counts for three of these species are odd multiples of ten: 2n=30 for E. suaveolens (Guzik and Lavkovsky, 1979); 2n=50 for E. pseudosclerantha (de Wet, 1960) and 2n=70 for E. montufaria (Bowden and Senn, 1962). All these chromosome numbers are from mitotic counts. The other ten species include species which have different chromosome races: E. cilianensis with 2n=20, 30, 40,

60, 70; E. curvula with 2n=20, 50, 60, 70, 80; E. echinochloidea with 2n=30 and 40; E. haborantha with 2n=60 and 90; E. lehmanniana with 2n=40, 50, 60; E. minor with 2n=20, 30, 40, 60; E. pilosa with 2n=20, 40, 50, 60; E. robusta with 2n=70 and 80; E. tremula with 2n=20, 30, 40 and E. unioloides with 2n=20, ca.30 and 40.

Vorster and Liebenberg (1977) reported a very abnormal meiosis in the race of E. curvula having 2n=50. Considering the wide range of polyploidy in E. curvula, the occurence of 2n=50 in that species may be the result of hybridisation between two chromosome races (4x x 6x for example). Apomixis has been reported for E. curvula and E. lehmanniana (Brown and Emery, 1958 and Streetman, 1963a) and this would allow the perpetuation of odd-euploid lines of hybrid origin. Larsen (1963) has reported the existence of considerable variability among E. unioloides and indicated that some races definitely are perennial while others are annual. He suggested that the plants of E. unioloides with 2n=ca.30 may be hybrids between the diploid and at the time hypothetical tetraploid. He also mentioned that the seed set of this race was very good. Chromosome counts of 2n=40 has since been reported for this species (Mehra et al., 1968).

The chromosome number of 2n=50 reported for E. pilosa by Mukherjee (1978) needs some explanation. He studied the meiotic behaviour of this species and reported a regular meiosis with twenty-five bivalents. It should be mentioned that there is a difference between the size of the chromosomes of the two accessions of E. pilosa studied by the present author and those of E. pilosa studied by Mukherjee (see Chapter 3). As has been mentioned earlier, the identification of Eragrostis species is difficult and there may be a misidentification of the species studied by Mukherjee, especially as he has not mentioned anything about identification or the deposition of voucher specimens. He has assumed that polyploid series based upon multiples of 4, 5 and 6 as the basic set are involved in this species, considering the previous counts of 2n=60 by Bowden and Senn (1962) and 2n=40 by Ono and Tateoka (1953). Mehra et al. (1968) also have suggested that the base number in the genus Eragrostis should be considered to be five because of their meiotic count of n=35 in E cilianensis. They mention that meiosis was quite normal in this race. The base number of five does occur in other tropical grass tribes: Andropogoneae, including Maydeae (Celarier, 1956), but it has not been reported in genera closely allied to Eragrostis. It may be that ten is a secondary base number in the genus, arising from the primary base

number of five. Because of the lack of strong evidence for five to be the base number of Eragrostis, it has seemed best to me to retain x=10 as the base number for the purposes of discussion.

2.4.3 The frequency of polyploidy in the genus

The high proportion of polyploid species and races in Eragrostis (76%) corresponds well with grasses generally, for Stebbins (1956) estimated that about 70% of grass species were polyploid.

Eragrostis is notable for the relatively high percentage of species for which more than one chromosome number has been reported (29%) (Table 2.5). This is too large to be attributed to taxonomic misidentification alone, even allowing for the taxonomic difficulties in the genus. Although taxonomic work in future may reduce the percentage, further cytological studies through the range of species can only increase it. These two effects will probably counteract each other and the percentage prove to be reliable. On occasions, such chromosome races have even been found in plants collected from the same area (eg. E. unioloides with 2n=20 and 2n=ca.30; E. cilianensis with 2n=20 and 2n=40; and E. zeylanica with 2n=40 and 2n=60, all these being counts from Payap in Thailand made by Larsen (1963). Larsen also reported 2n=ca.40 and 2n=ca.80 both from

Table 2.5 The relative frequency of *Eragrostis* species with one or more reported 'ploidy levels

| | Numbers of species | % |
|---|---|---|
| Species having both diploid and polyploid races | 22 | 18.4 |
| Species having no diploid race but having at least tetraploid races | 10 | 8.3 |
| Species having neither diploid nor tetraploid races, only higher levels of polyploidy being present | 3 | 2.5 |
| Species having more than one level of 'ploidy (=total of above categories) | 35 | 29.2 |
| Species with only one level of 'ploidy | 85 | 70.8 |
| Total number of species | 120 | 100 |

Prachinhuri in Thailand.

2.4.4 Aneuploidy

Among the Eragrostis species which have been cytologically examined (Appendix 1), aneuploidy has been reported for seventeen species (14%). An aneuploid chromosome number for three of these species has been reported only once and it is the only chromosome count for these species: 2n=44 for E. grandis (Skottbery, 1953); 2n=84 for E. swalleni (Gould, 1968); and 2n=72 for E. airoides (Davidse and Pohl, 1974). As it is sometimes difficult to distinguish univalent and bivalent chromosomes in meiotic divisions, (dot-shaped univalents and rod-shaped bivalents confuse the distinction). Pienaar (1953) also experienced this difficulty and noted that it was also difficult to distinguish between multivalents of small chromosomes and bivalents of large chromosomes in Eragrostis species. For these reasons aneuploid counts should be treated with caution. Davidse and Pohl (1974) have mentioned that E. airoides has been variously placed by authors in Sporobolus (as S. barasiliensis on the basis of having only one flower) or Eragrostis (on the basis of having a three-nerved lemmas). They suggested that since the base number of genus Eragrostis is x=10 and the base number of Sporobolus is x=6 or 9, E. airoides with 2n=72 has a much closer relationship to Sporobolus.

Aneuploid counts are associated with euploid counts in eleven other Eragrostis species, with euploid counts predominant. Larsen (1963) reported 2n=36 for E. zeylanica and has commented "Most difficult to explain is the Doi Sutep strain with 2n=36 chromosomes, all other numbers form a clear 10 series". This author has reported five other counts for this species, all multiples of 10 (Appendix 1).

The chromosome count of 2n=41 was made by the present author on E. heteromera and E. tenuifolia. The possibility of the extra chromosome being a B chromosome (accessory chromosome) was rejected in both species because firstly, of its existence in the root-tip cells of all three plants which were studied of both E. heteromera and E. tenuifolia; secondly, the extra chromosome was not smaller than others, on the contrary in E. heteromera the extra chromosome was similar in size to the largest A chromosome and in E. tenuifolia it was similar in size to the medium-sized chromosomes (Fig.3.4); and thirdly, the extra chromosome did not show a greater degree of heterochromatization. According to Stebbins (1971), these are the chief differences between B and A chromosomes. The chromosome number of one plant produced by selfing 2n=41 plants was also observed to be 2n=41 in E. heteromera. For plants to stabilise themselves with this chromosome number, they must have a non-sexual reproductive system.

Apomixis has been reported for E. heteromera (Brown and Emery, 1958). As it was mentioned earlier, apomixis has been reported for E. chloromelas and E. curvula (Brown and Emery, 1958 and Streetman, 1963a). Aneuploid counts have been reported for all three species (Appendix 1). A chromosome count of 2n=58 was determined for E. atrovirens by the present author. The other reported chromosome numbers for this species are 2n=40 and 60 (Appendix 1). It appears that the aneuploid plant of E. atrovirens has arisen by losing two chromosomes ("polyploid-drop").

2.4.5 Nature of Polyploidy

The occurrence of regular meiosis in three accessions of the tetraploid species E. tef (75-7, 75-12 and 75-93) in the tetraploid E. pilosa and in hexaploid E. mexicana indicates an allopolyploid origin for these species.

Tareke Berhe (1981) on the basis of the disomic inheritance of lemma colour, seed colour and panicle form in crosses betweeen different varieties of t'ef, tentatively suggested that t'ef is allotetraploid. The cytological observations presented here support that conclusion.

The morphological similarity between the sterile plant of E. minor (75-69) and the artificial hybrid which was synthesised by the present author between E. cilianensis (75-168) and E. minor (75-88) (see Chapter 5) is paralleled by the meiotic behaviour of these plants. I consider it likely that the sterile plant of E. minor (75-69) was a natural hybrid which arose at the Botanic Garden. Such hybridisation between sympatric Eragrostis species may not be uncommon and in turn explains the origin of the allopolyploids. The acknowledged difficulty in the identification of some species of Eragrostis may be due to interspecific hybridisation (whether or not it is followed by polyploidy) blurring the distinction between species.

The partial sterility of E. minor (75-88), which varies through the year, seemed to be more physiological rather than cytological, with a strong environmental effect attributable to seasonal differences in light intensity and temperature.

Pienaar (1953) studied the meiotic behaviour of seventeen perennial species of Eragrostis. Although he found regular meiosis in the diploid species, in nearly all the polyploid species he noticed a certain amount of meiotic irregularities. These included: the formation of multivalents, the existence of univalents and the lagging of chromosomes. He also noticed the close

resemblance between the meiotic behaviour of those wild polyploids and of an artificial autotetraploid which he produced with Colchicine from E. plana. He therefore suggested that the natural tetraploids are autopolyploids or segmental-allopolyploids, and the higher polyploids are auto- or autoallo-polyploids. Pienaar mentioned that meiosis in his synthetic autotetraploid E. plana was regular apart from up to two multivalents at metaphase I and one to three laggards at anaphase I which occurred in some pollen mother cells. He suggested that the high frequency of bivalents in the autotetraploid is probably due to the small size of the chromosomes and low chiasma frequency in Eragrostis species. Pienaar also mentioned that the seed-set of the synthetic autotetraploid was "excellent and not at all inferior to that of its diploid progenitor".

Vorster and Liebenberg (1977), studied meiotic behaviour in the Eragrostis curvula complex from Transvaal. They suggested that polyploids in these species are probably segmental-allopolyploids because they observed chromosome bridges, indicating heterozygosity for paracentric inversions, in some collections and what they interpreted as heteromorphic bivalents in others. Unfortunately it is not always possible to distinguish between auto- and allo-polyploids on the basis of pairing relationships of chromosome in meiosis. There are other factors which

affect chromosome pairing other than similiarity between chromosomes themselves alone such as: genes which regularise meiosis, length of the chromosomes, to which chiasma frequency is proportionate, (Darlington, 1965) and severe alternations of external conditions (Stebbins, 1971). Therefore Stebbins' (1971) caution: "the presence or absence of multivalent configurations in a natural polyploid may provide some indication as to whether or not it is of hybrid origin, but by itself this criterion is by no means decisive". Other information which is of use for distinguishing between auto- and allo-polyploids include: external morphology, biochemical differences, chromosome morphology, whether tetrasomic inheritance occurs and experimental synthesis of polyploids. Apart from the demonstration of disomic inheritance in t'ef (Tareke, 1981), none of this detailed information is at present available for any Eragrostis species. The potential for future studies is great.

# CHAPTER 3

# KARYOTYPES

## 3.1 Introduction

The chromosomes of Eragrostis are small and, at least in plants grown in a temperate climate, are technically difficult. The author found that the chromosomes usually clump together and were difficult to spread. This difficulty of obtaining a good preparation has been experienced by other authors: Pienaar (1953) and Leigh (1980) both report it. Leigh mentioned that the difficulty in spreading chromosomes and the overlapping of such small chromosomes made it hard for him to make accurate counts for the Eragrostis species which he studied (Appendix 2). These difficulties could be the reason why there is very little information on chromosome morphology in this genus.

Among the published surveys of the cytology of the Eragrostis species only two papers descibe the karyotypes. The karyotype of E. tremula has been figured by Mulay and Leelamma (1956) and the karyotype of E. pilosa by Mukherjee (1978) (Fig. 3.1). Both are based upon drawings of chromosomal preparations.

3.2 Method

The karyotypes were prepared from untouched photographs of metaphase chromosome of fifteen Eragrostis species, enlarged to x9500. Each chromosome was cut out individually and arranged in pairs, beginning with the largest. Where the nucleus was aneuploid the extra chromosomes were put next to the chromosome pair which they most resembled. All the photographs used were from preparations of colchicine-treated root tips. Each karyotype comprises the chromosomes of a single cell. As the sizes of chromosomes in each species often grade almost imperceptibly, and because there is little morphological difference between them, it was sometimes difficult to decide which chromosomes to put together. It was also not always easy to decide into which category to put chromosomes because of their small size and the limits of resolution of the optical microscope.

Occasionally the appearance of part of a chromosome has been modified (darkened) by the overlapping of another chromosome (an example of this may be seen in the second chromosome from the left in the karyotype of E. tenuifolia in Plate 3.4). The terminology used in describing the chromosome type is that of M.J.D.White as expanded by John and Lewis (1968). In Eragrostis acrocentrics were easily recognised by their very

unequal arms. Additionally they often carried satellites. The distinction between the true metacentric and submetacentric condition is somewhat arbitrary, because of the occurrence of intermediate conditions and the difficulty in determining the shape of such small, highly condensed chromosomes. Where the arms of the chromosome were recognisably different in length, the chromosomes were considered to be submetacentric.

Although the primary constriction was usually recognisable, secondary constrictions were not recognisable. Apparent secondary constrictions observed in one pair of the chromosomes of E. tef were more likely to be the nucleolar-organiser regions of satellited chromosomes; this was certainly the case in preparations of E. racemosa where the satellited chromosomes, which are known to be present from other preparations, were only visible as "secondary constrictions". Satellites were also difficult to observe except in favourable preparations. Where they had been seen in another cell, their occurrence has been recorded even though they may not be visible in the figured karyotype.

Heterochromatic regions were only observed on incompletely condensed chromosomes of one species: such regions appeared to be mainly on the longer chromosomes

but, because no more information was available for comparison, no attempt has been made to describe the portion of the heterochromatic regions. They were useful, however, as an extra source of information when pairing up the chromosomes of that species (E. tenuifolia) in preparing a karyotype.

The fifteen species whose karyotypes were studied, included eight diploids (Plate 3.1), three tetraploids (Plate 3.2), one hexaploid (Plate 3.3) and three aneuploids (Plate 3.4). The eight diploids were E. aethiopica, E. bicolor, E. ciliaris, E. gangetica, E. namaquensis var. diplachnoides (two accessions, 75-65 and 75-161), E. patens, E. plana and E. racemosa. The tetraploid species were E. tef (two accessions 75-7 and 75-6), E. pilosa and E. superba. E. mexicana was the hexaploid species whose karyotype was studied and the three aneuploid plants belonged to E. heteromera (2n=41), E. tenuifolia (2n=41) and E. atrovirens (2n=58). Of these species, E. aethiopica, E. bicolor, E. heteromera and E. mexicana are considered to be close relatives of E. tef (Jones, Ponti, Tavassoli and Dixon, 1978).

## 3.3 Results and Discussion

The karyotypes are displayed in Plates 3.1 to 3.5 and some data from them is given in Table 3.1. The numbers of metacentrics and submetacentrics given in this table are, owing to the limitations described in "Methods", somewhat tentative.

### 3.3.1 Diploids (Plate 3.1)

Eragrostis aethiopica is unusual in having a karyotype without any acrocentric chromosomes. One or two pairs of these occur in most Eragrostis karyotypes and are also often satellited. Instead, in this species only the submedian and median chromosomes occur.

Satellites were recognisable on one pair of longer chromosomes of E. bicolor. E. ciliaris too had one pair of satellited chromosomes, although they were not quite the largest - maybe because they were not fully flattened. It is interesting to note that E. plana and E. racemosa, among the diploids, also had long satellited chromosomes. E. patens in contrast had the satellites on one pair of its medium-sized chromosomes.

E. gangetica had the smallest chromosomes among the diploids and indeed among all the species whose karyotypes were studied: its largest chromosomes were no more than 1.4 microns in length; only E. heteromera

(2n=41) parallels it in this respect, though its chromosomes were appreciably fatter. The ratio of the largest to the smallest chromosome in E. gangetica was 1.5 which is the lowest ratio among the species studied.

There was close correspondence between the karyotype of the two acquisitions of E. namaquensis var. diplachnoides, though the studied cell of accession 75-161 had more condensed chromosomes. Three pairs of chromosomes were acrocentric, making this species unique among those studied.

de Winter (1960) mentioned that, according to another observer (de Wet) E. namaquensis has smaller chromosomes than other Eragrostis species. In contrast, the chromosomes of E. namaquensis var. diplachnoides studied by the present author not only were not smaller than the chromosomes of other Eragrostis species studied, but were among the largest chromosomes observed in the genus. Tateoka (1965b), commented that the chromosomes of the plants of E. namaquensis studied by him were two to four times as long as those of other Eragrostis species; an even more extreme case. Christopher and Abraham (1974), who also reported the chromosome number of E. namaquensis var. diplachnoides mentioned that the length of the chromosomes was between 1.5 and 3.5 microns for this species. This was larger than for the other species they studied: E. atrovirens

(1.5-2.5μm), E. japonica (1.5 to 2.5μm) and E. unioloides (1.0 to 2.0μm).

Unfortunately these author's illustrations provide no detailed information. Non-standardisation of pretreatment and preparation techniques may account for the reported differences, but, where the same technique has been applied, E. namaquensis has chromosomes larger than most.

E. patens and E. plana both have their largest chromosomes 2 microns in length. Their smallest chromosomes are also similar in length (1.2, 1.3 microns), but they differ in the satellite-bearing acrocentrics: in E. patens the satellites are on one pair of medium-sized chromosomes, whereas in E. plana the satellites are on the largest pair of chromosomes. The chromosomes of E. plana are also thicker than those of E. patens. Pienaar (1953) reported that E. plana had chromosomes of 1 to 2 microns in length: my calculations more or less confirm those dimensions.

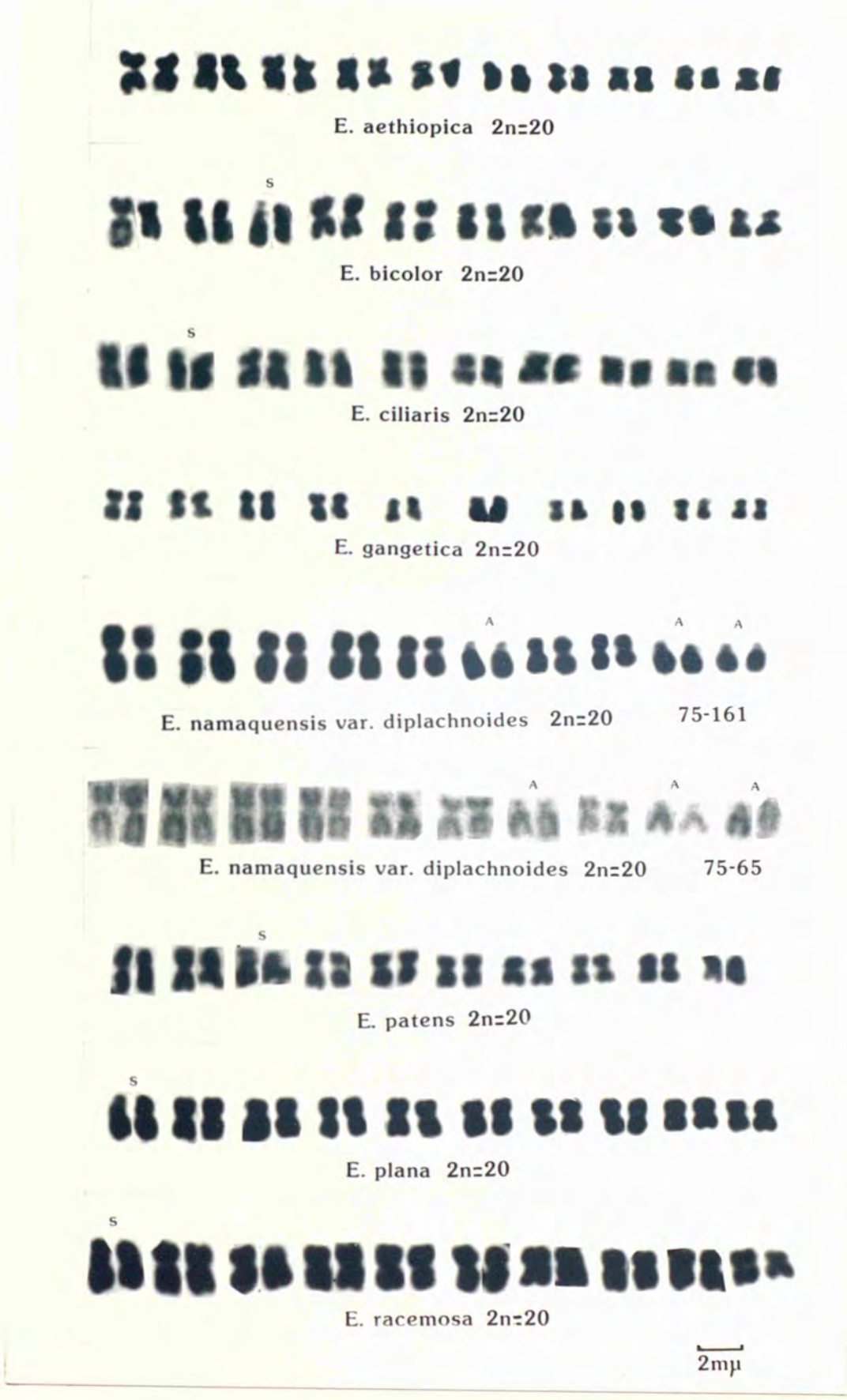
E. racemosa differs from the other diploids in having thick as well as long chromosomes. E. namaquensis var. diplachnoides has equally long chromosomes, but they are somewhat thinner even in the condensed state.

PLATE 3.1 Karyotypes of eight diploid species of Eragrostis.

S = Satellited chromosomes.

A = Acrocentric chromosomes.

For details of the somatic cells from which these karyotypes were prepared refer, in the same order to Plates: 2.1A, 3.6B, 3.6C, 2.3E, 2.4B, 2.4A, 2.4C and 2.4D.


E. aethiopica 2n=20
S
E. bicolor 2n=20
S
E. ciliaris 2n=20
E. gangetica 2n=20
A
A
A
E. namaquensis var. diplachnoides 2n=20 75-161
A
A
A
E. namaquensis var. diplachnoides 2n=20 75-65
S
E. patens 2n=20
S
E. plana 2n=20
S
E. racemosa 2n=20
2mμ

3.3.2 Tetraploids (Plate 3.2)

The two karyotypes of E. tef differ, because only one preparation (75-7) is fully contracted, the other (75-6) not only has longer chromosomes, but the range of chromosome size is greater (the ratio of largest to smallest is 2.6 for these less condensed chromosomes, it is 2.0 for the completely condensed karyotype). In Chapter 2 the Plate 2.5 of 75-6 shows its fully contracted chromosomes. They are very similar in size to those of 75-7. This demonstrates that the size differences are indeed due to incomplete condensation. One line of E. tef (75-6) is notable for having four satellited acrocentric chromosomes; in the other karyotyped line (75-7), no satellited chromosomes were seen. It is not clear whether this is a real difference or due to practical difficulties of observing the satellites. Commonly most or all the dividing cells of a preparation would not show satellites even though these were known to be present. The presence of four satellites, if widespread in t'ef, could indicate that this species is of recent origin with satellited chromosome duplication being the result of polyploidy. It is relevant, in this respect, to note that the other t'ef line which was karyotyped (75-7) had four acrocentric chromosomes of the type normally associated with satellites in Eragrostis, although satellites were not recognised on them. The chromosomes of E. tef are

small even by the standards of the genus: the smallest are dot-shaped.

E. pilosa has a similar karyotype to E. tef having a similar size gradation of very small chromosomes. They differ in E. tef having four acrocentric chromosomes, whereas in E. pilosa only two were observed, although another pair of medium size chromosomes in E. pilosa might also be acrocentric. Fernandes and Queiras (1969) also reported one pair of satellites in E. pilosa. Some of the medium-sized chromosomes of E. pilosa and E. tef resemble the smaller chromosomes of E. aethiopica. These species are believed to be related (Jones, Ponti, Tavassoli and Dixon, 1978).

Mukherjee (1978) has reported a chromosome number of 2n=50 for E. pilosa (Appendix 1) and has done the karyotype of this species (Figure 3.1).

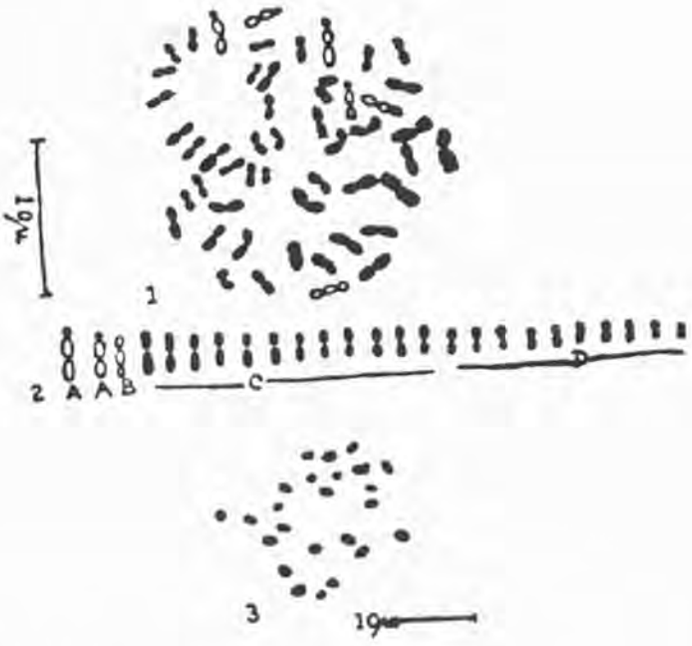



Figure 3.1 Mukherjee's figure of mitosis, and meiosis karyotype for E. pilosa (1978).

He gave the length of the largest chromosome as 3.3 microns and 1.3 for the shortest. The size of the chromosomes of E. pilosa reported by Mukherjee is much larger than that reported by all other observers for other species, apart from E. namaquensis var. diplachnoides (Christopher and Abram, 1974). The drawing of the chromosomes of E. pilosa in Fernandes and Queires' paper (1969) shows that the largest chromosome is less than 2 microns in length. The large size of chromosomes of E. pilosa reported by Mukherjee may perhaps be attributed to his use of Aesculine, rather Colchicine, as a pre-treatment. However, the length of untreated chromosomes in my own preparations was still less than three microns. It is possible that Mukherjee

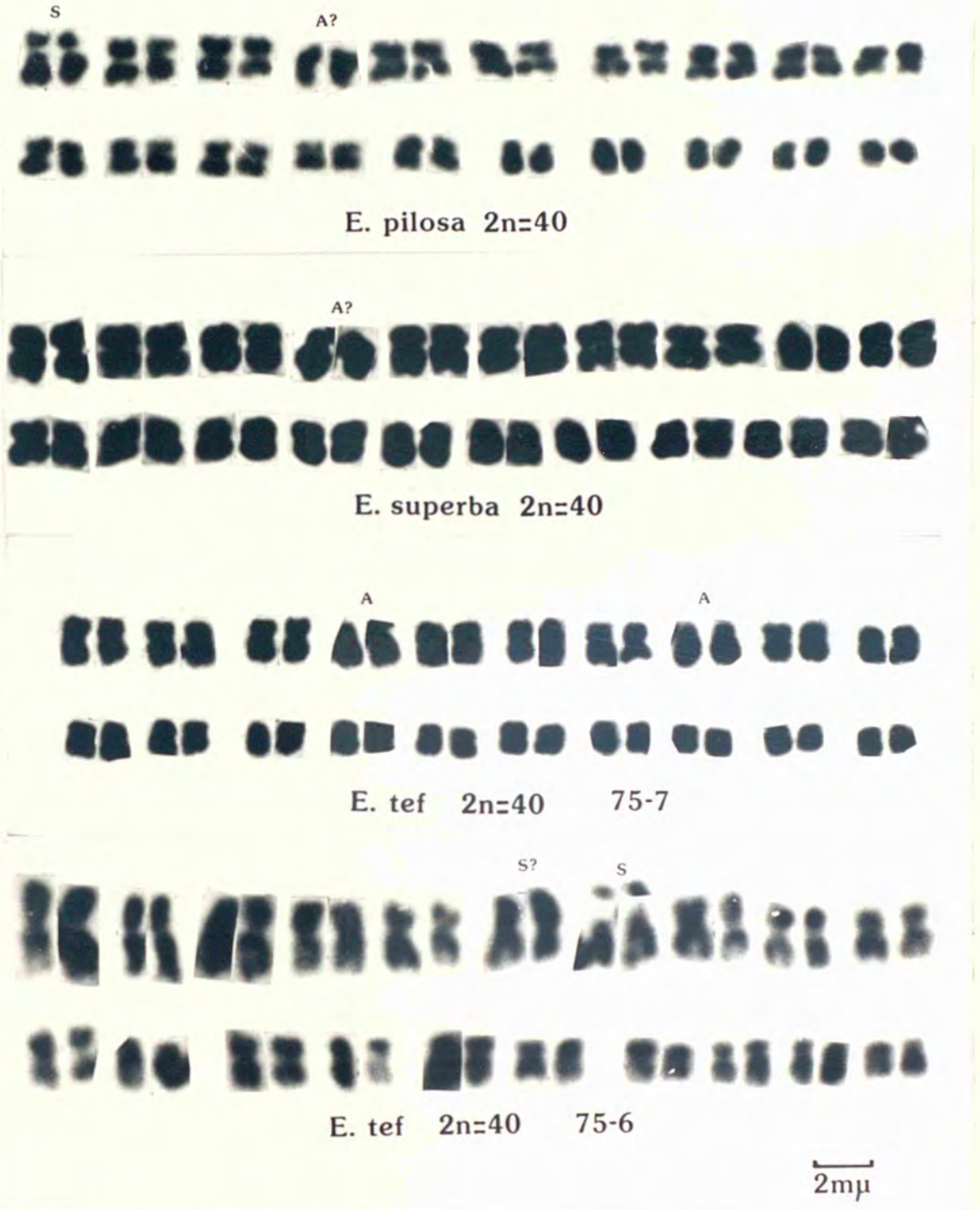



PLATE 3.2 Karyotypes of three tetraploid species of Eragrostis

S. = Satellited chromosomes

A = Acrocentric chromosomes.

For details of the somatic cells from which these karyotypes were prepared refer, is the same order to Plates: 2.5D, 3.6D, 2.5C and 3.6A.

misidentified his material: his is the only count of 2n=50 for E. pilosa, and the secondary constrictions he shows in his drawing have not been reported for any Eragrostis species. Alternatively he may have reported incorrect measurements. In either case it would seem appropriate for his observations to be repeated.

Among the species whose chromosomes were investigated E. superba had the thickest chromosomes of all. The longest chromosome of E. superba was 1.8 microns long; the shortest was 1.2 microns. Pienaar (1953) reported a chromosome length of 1.0 to 1.8 microns for E. superba which closely agrees with the present results. Except for one pair of the chromosomes of E. superba which could be considered acrocentric, the rest of the chromosomes were meta- and submetacentric.

### 3.3.3 Hexaploid (Plate 3.3)

The hexaploid E. mexicana was notable for its two pairs of satellited chromosomes, perhaps indicating a recent polypoid origin. Since meiosis in this species was regular (Chapter 2), allopolyploidy is more likely to have been involved than autopolyploidy. The most plausible explanation involves diploid and tetraploid progenitors, each contributing a pair of satellited chromosomes; another pair (perhaps two pairs) of acrocentric chromosomes is present and these may be the

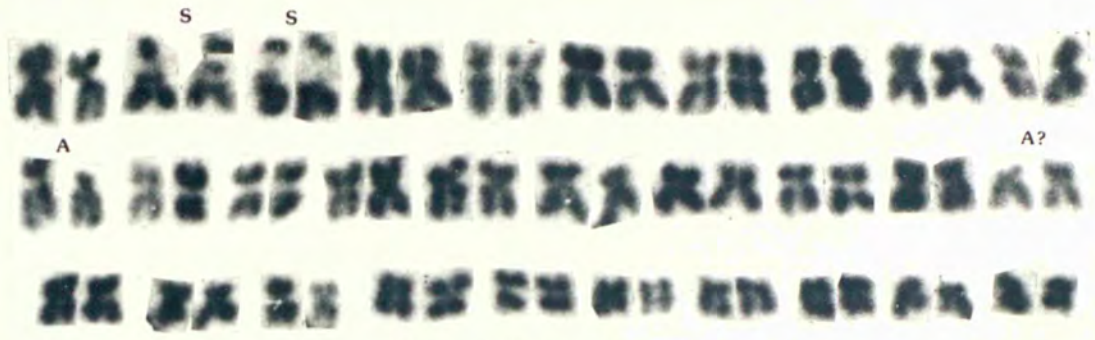



PLATE 3.3 Karyotypes of a hexaploid species of Eragrostis

S = Satellited chromosomes.

A = Acrocentric chromosomes

For details of the somatic cell from which this karyotype was prepared refer to Plate 2.9 top.

remains of formerly satellited chromosomes.

3.3.4 Aneuploids (Plate 3.4)

E. heteromera and E. tenuifolia were particularly notable for one extra chromosome in addition to an otherwise normal tetraploid complement. In E. heteromera this additional chromosome was the same size as the largest pair, but in E. tenuifolia it was similar to the ninth, medium sized pair. The karyotype of E. heteromera has similarities to that of E. tef, to which it is considered to be related (Jones et al., 1978), but is not as similar as E. pilosa for example. However, it differs from these in having no clearly distinguishable satellited or acrocentric chromosomes.

The incompletely condensed chromosomes of the preparation of E. tenuifolia showed heterochromatic regions. This aneuploid had two pairs of acrocentric chromosomes and it was not possible to distinguish satellites on them. The two chromosomes of pair 6 show different morphology: their arm length, position of centromeres and heterochromatic regions do not correspond. It is possible that a pericentric inversion has occurred, the studied plant being heterozygous for the inversion (see Fig. 3.2 for interpretation).

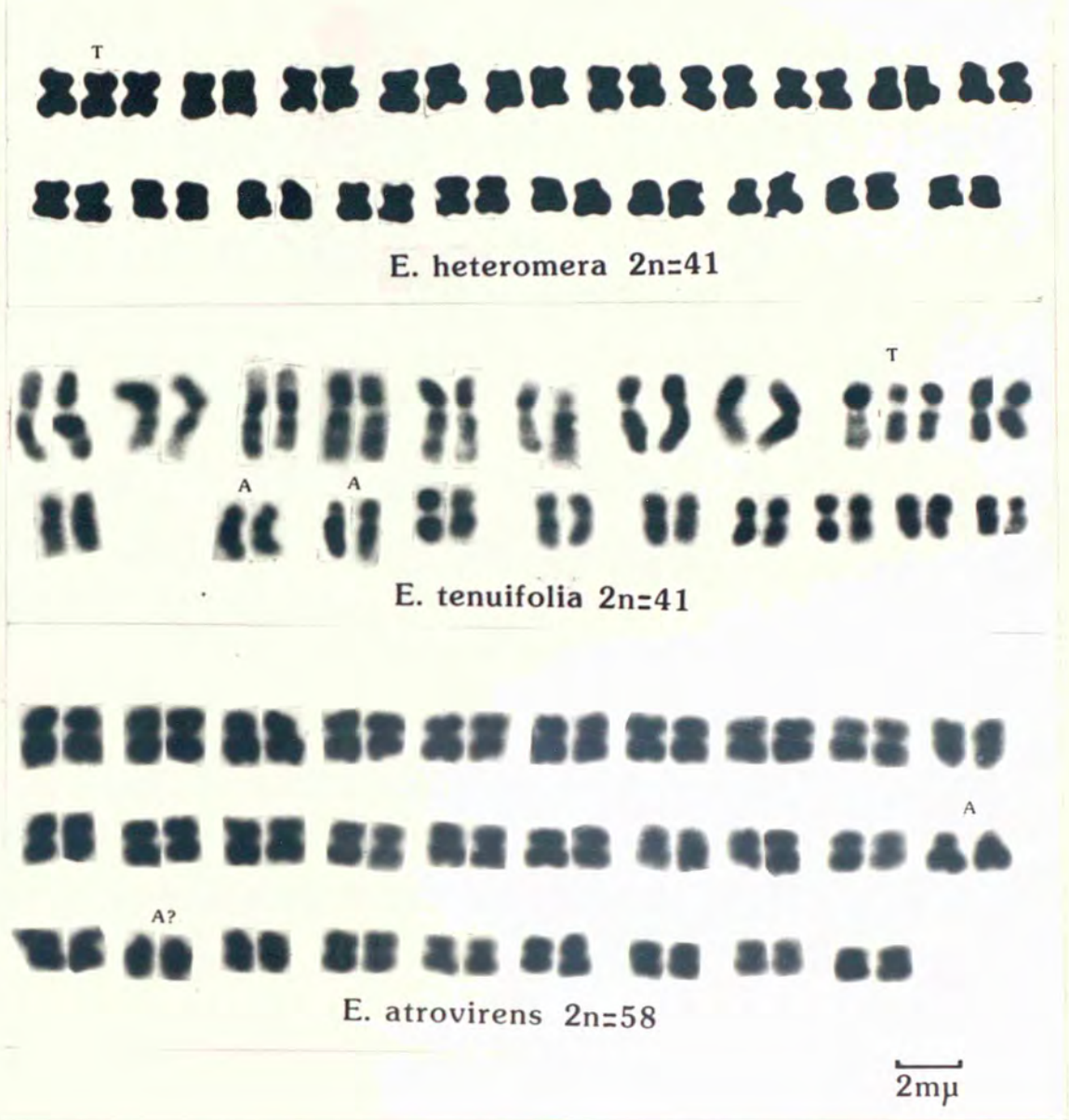



PLATE 3.4 Karyotypes of three aneuploid species of Eragrostis

T = Trisomic chromosomes.

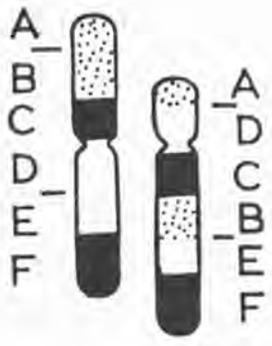
A = Acrocentric chromosomes.

For details of the somatic cells from which these karyotypes were prepared refer to Plates: 2.10D, 2.2D and 2.2A.



R.B.G.N.C.
LIBRARY

Figure 3.2 Interpretative diagram of chromosome 6 of karyotype of E. tenuifolia. The structural difference may be explained by a pericentric inversion of the region between the lines.




The maintenance of both these conditions (aneuploidy and inversion heterozygosity) can be explained by apomixis. It is relevant to note that apomixis has been reported in E. heteromera (Brown and Emery, 1958) which is also aneuploid (see also Chapter 2).

The chromosomes of E. atrovirens (2n=58) were relatively small, the largest ones being only 1.6 microns in length. This species had one pair of medium-sized and clearly distinguishable acrocentric chromosomes and possibly another pair of medium-sized acrocentrics. In their size and form the karyotype resembles that of t'ef, although the two species are not considered, on other characters, to be closely related (Ponti, 1978).

PLATE 3.5 Karyotypes of Eragrostis tef and closely related species.

S = Satellited chromosomes.

A = Acrocentric chromosomes.

T = Trisomic chromosomes.

For details of the somatic cells from which these karyotypes were prepared, refer to Plates: 2.1A, 3.6B, 2.5D, 2.5C, 3.6A and 2.10D.


E. aethiopica 2n=20
S
E. bicolor 2n=20
S
A?
E. pilosa 2n=40
A
A
E. tef 2n=40 75-7
S?
S
E. tef 2n=40 75-6
T
E. heteromera 2n=41
S
S
A
A?
E. mexicana 2n=60
2mμ

PLATE 3.6 Somatic cells from which some of the karyotypes were prepared.

A. *E. tef* 75-6 see Plates 3.2 and 3.5

B. *E. bicolar* see Plate 3.1

C. *E. ciliaris* see Plate 3.1

D. *E. superba* see Plate 3.2

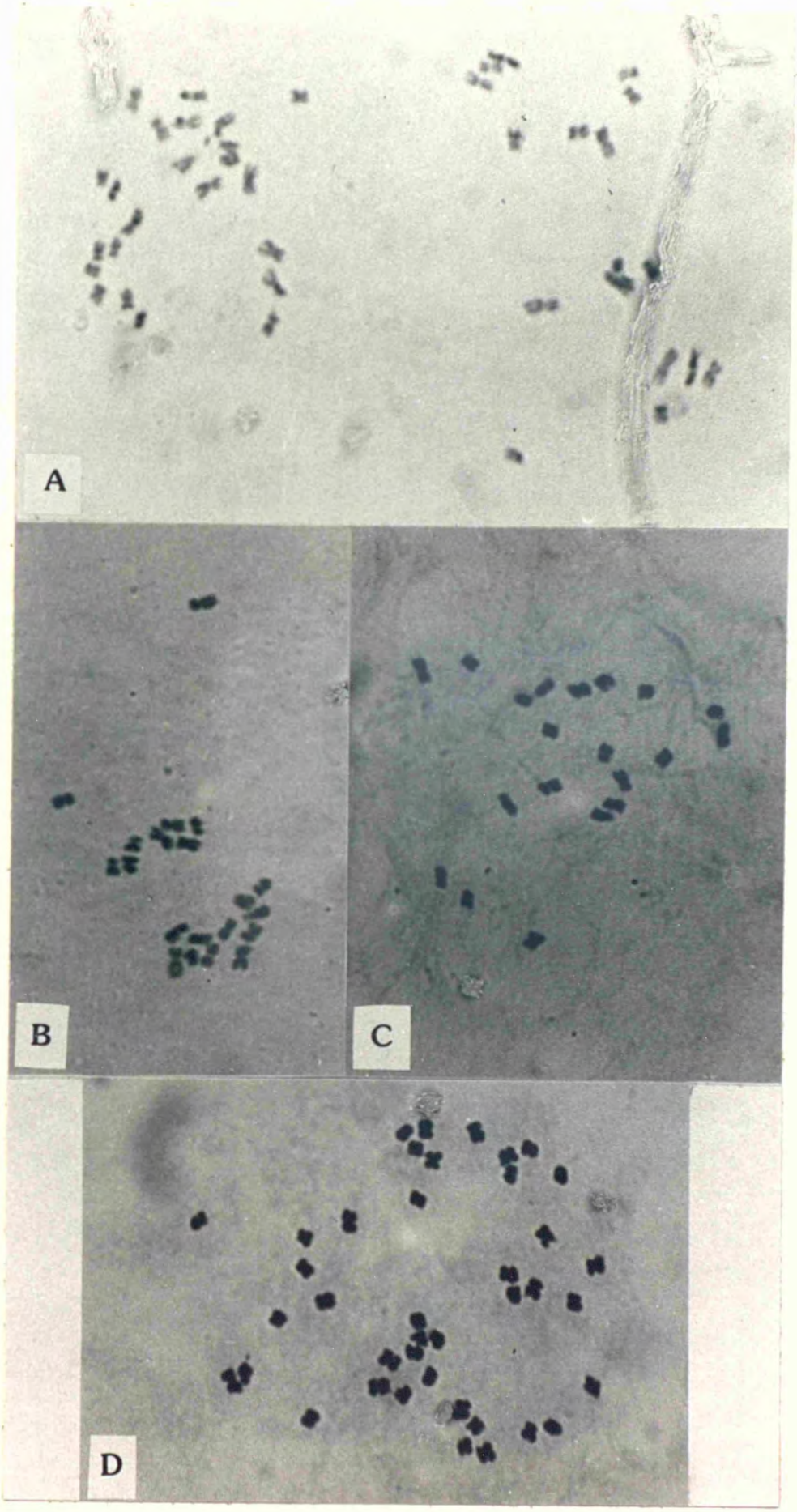

A
B
C
D

Table 3.1 Summary of data from karyotypes of some Eragrostis species (Observation of metaphases of root-tip mitoses after Colchine pretreatment)

| Species | Dimension of Chromosomes (µm) | | Chromosome types | |
|---|---|---|---|---|
| | Largest | Smallest | SAT chromosomes (when observed) | Centromere position on other chromosomes |
| Diploids (2n=20) | | | | |
| E. aethiopica | 1.6 | 0.9 | n.o. | Median and submedian |
| E. bicolor | 2.2 | 1.3 | 2, long, acrocentric | Mostly submedian |
| E. ciliaris | 1.9 | 1.0 | 2, median, acrocentric | Mostly submedian |
| E. gangetica | 1.4 | 0.9 | n.o. | Median and submedian |
| E. namaquensis var. diplachnoides | | | | |
| 75-161 | 2.3 | 1.4 | n.o. | 6 acrocentric and remainder mostly submedian |
| 75-65 | 2.4 | 1.5 | n.o. | 6 acrocentric and remainder mostly submedian |

| | | | | |
|---|---|---|---|---|
| E. patens | 2.0 | 1.2 | 2, medium, acrocentric | Median and submedian |
| E. plana | 2.0 | 1.3 | 2, long,acrocentric | Mostly median |
| E. racemosa | 2.3 | 1.3 | 2, long, acrocentric | Median and submedian |
| Tetraploids (2n=40) | | | | |
| E. tef 75-7 | 1.6 | 0.8 | n.o. | 4 acrocentric and remainder median and submedian |
| " 75-6* | 2.9 | 1.1 | (2) 4?, medium, acrocentric | Median and submedian |
| E. pilosa | 1.6 | 0.8 | 2, long, acrocenric | 2? acrocentric and remainder median and submedian |
| E. superba | 1.8 | 1.2 | n.o. | 2? acrocentric and remainder median and submedian |
| Hexaploid (2n=60) | | | | |
| E. mexicana | 2.1 | 0.9 | 4, long, acrocentric | (2) 4? acrocentric and remainder mostly submedian |
| Aneuploids | | | | |

| | | | | |
|---|---|---|---|---|
| E. heteromera (2n=41) | 1.5 | 0.9 | n.o. | median and submedian |
| E. tenuifolia* (2n=41) | 2.8 | 1.1 | n.o. | 4, acrocentric and remainder mostly median |
| E. atrovirens (2n=58) | 1.6 | 0.9 | n.o. | (2) 4? acrocentric and remainder median and submedian |

* The chromosomes in these preparations were partially contracted

n.o. = not observed

3.3.5 General

Among the species whose karyotypes were studied, some were relatively distinct. For example, the diploid E. namaquensis var. diplachnoides with three pairs of acrocentric chromosomes, differed from all the other diploid species, which had only one pair of acrocentric chromosomes, or none (as E. aethiopica and E. gangetica). The karyotype of E. gangetica had very distinctive chromosomes appreciably shorter and more slender than any other species examined. E. superba and to a lesser extent E. racemosa had much thicker chromosomes than the other species studied. The remaining species were much less distinct in their karyotypes, but their karyotypes do differ in the length and thickness of chromosomes, the number of acrocentrics, the number of satellites and in the relative numbers of metacentric and submetacentric chromosomes. Such differences in karyotype between Eragrostis species ought to throw some light on the relation between species.

Ponti (1978) studied the taxonomy of some species of Eragrostis and put E. gangetica and E. patens together in her group 1, particularly on the basis of epidermal characteristics. However, the chromosomes of E. patens are appreciably larger than those of E. gangetica and these species are morphologically very

distinct. The cytological evidence here suggests that Ponti's group 1 may be heterogenous. Ponti also allied E. superba, which has very thick chromosomes, to the species of group 1. She mentioned that this species differed from the rest of group 1 in its micro-hairs and in having completely different caryopses and external morphology. E. superba is equally distinct in its karyotype from those group 1 species I studied.

Ponti (1978) put E. tenuifolia and E. plana in group 2 of her classification. The chromosomes of E. plana are shorter and thicker than the chromosomes of E. tenuifolia, and the smallest chromosome of E. plana is slightly longer than the smallest chromosomes of E. tenuifolia. It should be mentioned that since the chromosomes of the preparation of E. tenuifolia studied were not completely contracted, it is not possible to get a clear conclusion. In fully contracted preparations, which were, however, not good enough for karyotyping, the size of the chromosomes was closely comparable (Plate 2.7B).

E. namaquensis var. diplachnoides, with its large chromosomes and three pairs of acrocentric pairs, is very distinct from all the other species studied. de Winter (1960) decided, on morphological grounds, to put E. namaquensis in a new genus (Diandrochloa). This genus differs from Eragrostis in having membraneous

ligules; the ligule is ciliate, rarely membraneous, in other Eragrostis species. Its flowers have only two stamens, although some other Eragrostis species also have only two stamens including E. gangetica, whose karyotype has been described above. Ponti (1978) described some distinctive epidermal characters which separated E. namaquensis var. diplachnoides from thirty-eight other Eragrostis species which she studied. Bekele and Lester (1981), who studied the biochemical characters of some of these species, also found little similarity between the chromatographic data of this species and the other Eragrostis species he studied. Considering the karyotype of Eragrostis namaquensis and the comments of Ponti, de Winter and Bekele, perhaps this species should be excluded from the genus; if it is retained it certainly merits sub-generic status.

The comparison of the two varieties of E. tef is instructive. E. tef (75-6) is a short plant and late maturing, whereas E. tef (75-7) is a tall and early maturing variety. The other morphological differences between them are not very great and it is not surprising that their karyotypes are very similar, if allowance is made for the incomplete contraction of the chromosomes of the preparation of 75-6 (see also Plate 2.5B for confirmation of this view).

Five of the karyotyped species are considered by Jones *et al*. (1978) to be related to t'ef on morphological grounds. *E. aethiopica* (2x), *E. bicolor* (2x), *E. heteromera* (4x), *E. pilosa* (4x) and *E. mexicana* (6x). The karyotype of t'ef is generally similar to that of most of these species (Plate 3.5), but *E. heteromera* and to a lesser extent *E. bicolor* are the least similar of this group to t'ef. It may be significant that both these species, unlike the others, are perennials.

The species representing the genus, apart from *E. namaquensis* var. *diplachnoides*, are notably uniform in their chromosome morphology. The chromosomes are all small and predominantly metacentric and submetacentric, that is more or less symmetrical. Stebbins (1971, p.96) says "In the plant kingdom as a whole, symmetrical karyotypes are usually primitive. The predominant trend is from symmetry to greater asymmetry, though reversals of this trend occur periodically". On this hypothesis *Eragrostis*, which averages only one acrocentric per genome, and that often recognisable as a specialised nucleolar-organising chromosome (a satellite-bearing acrocentric), represents a primitive karyotype among grasses. This is confirmed by the morphology of the spikelets of *Eragrostis* which have many, similar florets, and by the grains which lack specialised structures for dispersal, characters which Stebbins

(1956) considers to be primitive in the family. Furthermore the flowers of Eragrostis mature acropetaly on the spikelet and the grains are naturally free-threshing, characters which also are likely to be primitive (they occur in Bambusoideae) (B.M.G.Jones, verbal communication).

# CHAPTER 4

# POLLEN GRAINS

## 4.1 Introduction

The size of pollen grains can be a useful indicator of chromosome number. Darlington (1937, page 221) stated that "where the external and developmental factors are equal, the size of the cell might be expected to be proportionate to the number of chromosomes of which the nucleus is constituted when the number is simply doubled or halved." Davidson (1975) mentioned that "an increase in cell size, whether subtle or obvious, seems to be a general result of an increase in chromosome numbers in plants and animals." Whether such a relationship exists in the genus Eragrostis has not yet been established.

Pienaar (1953) who studied the cytology of some Eragrostis species, made measurements of the pollen of five species, but failed to find a correlation between chromosome number and the size of pollen grains, though he noticed that an artificially produced autotetraploid of E. plana had significantly larger pollen than the diploid ancestor. Koch (1974) examined the pollen of some species of the Eragrostis pilosa-pectinacea group.

He concluded that "the use of pollen diameter to infer chromosome number is limited, however, by the fact that the pollen diameter of the octoploid population of E. frankii falls within the range of those of the hexaploids." Stalker and Wright (1975), who studied the reproduction system of E. curvula, measured the pollen grains of diploid E. curvula, artificially produced autotetraploid and natural tetraploid; they concluded that differences in pollen diameter were not adequate to distinguish the diploid from the tetraploids.

I examined pollen of most of the Eragrostis species whose chromosome numbers I had already been determined. The pollen of most of these species had not been studied previously.

## 4.2 Method

Pollen grains were collected from sixty accessions comprising thirty four Eragrostis species. Most of the Eragrostis species studied flowered early in the morning, especially on warm and bright days. For example E. tef flowers between 4 a.m. and 6 a.m. during the summer months in Britain and takes only a few minutes to complete anthesis. However it should be mentioned that pollination in E. tef is the fastest of all the species which were studied in this work. In order to obtain fresh pollen without contamination, it

was necessary to control the flowering so that several accessions could be sampled each day at a convenient time.

Plants were put into a dark cabinet between 5.30 and 7p.m. on the evening before the day that pollen was to be collected and were maintained at about +10°C over night. Between 8 and 9 a.m. the next morning plants were removed from the cabinet and the anthers were collected as the flowers opened. The anthers which were on the point of dehiscence were removed with jeweller's forceps and allowed to dehisce on a slide. The pollen was then immersed in a drop of lactophenol cotton-blue on the slide. Using a projecting microscope images of the pollen grains were projected onto a wall, where they were measured with a cut-out scale drawn from a previously projected image of a micrometer scale. Fifty pollen grains of each accession were measured, sampling different areas of the slide at random. Micrograins, shrunken and empty, or partially empty grains were ignored, as were occasional large grains (from dyad?). Only E. papposa presented special difficulties: few of its pollen grains were full and the filled grains differed greatly in size; the results for this species thus gave a more variable sample than usual.

The significances of the differences observed were estimated with the 't'-Test.

Four examples of comparisons of pollen diameter between accessions of a species, using Students' 't'.

| Species | Accessions | Difference between the means (µm) | SE (µm) | Value of 't' | Probability |
|---|---|---|---|---|---|
| E. tef | 75-7 with 75-6 | 2.7 | 0.4, 0.4 | 4.73 | $\ll$ .001 |
| " | 75-7 with 75-9 | 1.1 | 0.4, 0.7 | 1.97 | $<$ .05 $>$ .02 |
| E. minor | 78-6 with 75-69 | 2.9 | 0.5, 0.4 | 4.06 | $\ll$ .001 |
| " | 75-134 with 78-6 | 1.2 | 0.5, 0.5 | 1.64 | $>$ .1 |

## 4.3 Results

Tables 4.1 to 4.4 give the means of pollen diameter for the species examined. There was some variation within each sample, but the calculated standard errors of the means were relatively small. Pairs of species (or accessions) whose mean pollen diameter differ by over two microns are statistically significantly different (at $P < 0.01$). In those species where two or more accessions were examined, in about half the cases the difference between the samples were statistically significant (at $P < 0.01$). Thus the accessions 75-7 and 75-6, which have the smallest and greatest pollen diameters of the seven t'ef accessions examined, were very significantly different ($P << 0.001$). But 75-9, which has an intermediate value, is only just different from either extreme ($P < 0.05$, $> 0.02$ and $>> 0.1$).

The diploid *E. gangetica* (2n=20) had the smallest pollen grains of all the species studied (mean diameters of two accessions 9.1 and 9.9 μm). The largest pollen grains belonged to aneuploid *E. atrovirens* (2n=58): the mean pollen diameter in this species was 44 μm.

The mean pollen diameters in the fourteen diploid species lie between 21 and 35 microns (Table 4.1). Twelve of these mean diameters fall within the range 21-28 μm; the two others (*E. plana* and *E. racemosa*) have

Table 4.1 Pollen diameter (mean and standard error) of diploid Eragrostis species (n=50 grains)

| Species | (accession number) | $\bar{x}$(µm) | SE(µm) |
|---|---|---|---|
| E. aethiopica | (75-1) | 24.4 | 0.2 |
| E. aspera | (75-144) | 25.2 | 0.4 |
| E. bicolor | (75-94) | 23.6 | 0.3 |
| E. chapelieri | (75-167) | 25.3 | 0.3 |
| E. cilianensis | (75-140) | 25.0 | 0.4 |
| " " | (75-137) | 26.7 | 0.4 |
| " " | (78-5) | 27.9 | 0.3 |
| E. ciliaris | (75-125) | 24.3 | 0.5 |
| " " | (75-169) | 25.3 | 0.6 |
| E. gangetica | (75-64) | 21.1 | 0.3 |
| " " | (75-78) | 22.3 | 0.4 |
| E. minor | (75-75) | 25.0 | 0.6 |
| E. namaquensis var. diplachnoides | (75-65) | 24.5 | 0.4 |
| E. patens | (75-147) | 26.1 | 0.4 |
| E. plana | (75-95b) | 35.4 | 0.4 |
| E. racemosa | (75-124) | 35.3 | 0.9 |
| E. tenella | (75-81) | 22.6 | 0.4 |
| E. unioloides | (75-83) | 25.6 | 0.3 |

mean diameter about 35 μm.

The sixteen tetraploid species examined have mean pollen diameter between 22 and 41 microns (Table 4.2). Eleven of them lie between 25 and 34 μm; one has a diameter as low as 22 μm; the remaining four species have pollen diameters as great as 38-41 μm.

The three hexaploid species have mean pollen diameters between 33 and 37 microns (Table 4.3). The heptaploid and octaploid species have mean diameters of 35 and 40 microns respectively (Table 4.3).

Thus there is some relationship between pollen size and polyploidy: the diploids have the smallest pollen grains, the tetraploids are generally larger and the higher polypoloids have pollen grains which are amongst the largest recorded for the genus. Nevertheless there is considerable variation in size within each chromosome group and considerable overlap between them. This is shown diagrammatically in Figure 4.1.

The aneuploid species and races have pollen grains whose size correspond with that of their nearest euploid chromosome race or species (Table 4.4). Thus the pollen diameter of E. tenuifolia plants with 40 chromosomes is 27-29 μm; with 41 chromosomes it is 31 μm. E. heteromera, also with 41 chromosomes, has pollen of a similar size. However the pollen of plants

Table 4.2 Pollen diameter (mean and standard error) of tetraploid Eragrostis species (n=50 grains)

| Species | (accession number) | $\bar{x}$(µm) | SE(µm) |
|---|---|---|---|
| E. capensis | (75-18) | 40.5 | 0.8 |
| E. cilianensis | (75-168) | 30.8 | 0.4 |
| E. congesta | (75-145) | 25.4 | 0.3 |
| E. curvula | (75-73) | 38.5 | 0.4 |
| " " | (75-72) | 39.0 | 0.4 |
| E. kiwuensis | (75-107) | 26.0 | 0.4 |
| E. lehmanniana | (75-19) | 37.8 | 0.5 |
| E. minor | (75-69a) | 30.1 | 0.4 |
| " " | (78-7) | 30.3 | 0.3 |
| " " | (78-6) | 33.0 | 0.5 |
| " " | (75-134) | 34.2 | 0.5 |
| E. papposa | (75-113) | 22.3 | 0.3 |
| E. pilosa | (75-136) | 26.6 | 0.2 |
| " " | (75-163) | 27.5 | 0.4 |
| E. porosa | (75-130a) | 33.5 | 0.5 |
| E. rigidior | (75-130b) | 31.5 | 0.3 |
| E. schweinfurthii | (75-108) | 34.0 | 0.4 |
| E. superba | (75-128) | 40.0 | 0.5 |
| " " | (75-159) | 40.0 | 0.5 |
| " " | (75-173) | 40.5 | 0.6 |
| E. tef | (75-7) | 29.6 | 0.4 |
| " " | (75-93) | 30.6 | 0.5 |
| " " | (75-14) | 30.8 | 0.5 |
| " " | (75-9) | 31.2 | 0.7 |
| " " | (75-12) | 31.4 | 0.5 |
| " " | (75-117) | 31.7 | 0.7 |
| " " | (75-6) | 32.3 | 0.4 |
| E. tenuifolia | (75-98) | 27.2 | 0.3 |
| " " | (75-100) | 27.7 | 0.2 |
| " " | (75-105) | 28.8 | 0.4 |
| E. trichodes | (75-22) | 25.2 | 0.3 |
| " " | (75-21) | 26.7 | 0.4 |

Table 4.3 Pollen diameter (mean and standard error) of hexaploids and higher polypoid Eragrostis species (n=50 grains)

| Species | (accession number) | 2n | $\bar{x}$(µm) | SE(µm) |
|---|---|---|---|---|
| E. barrelieri | (74-1) | 60 | 33.2 | 0.5 |
| E. cilianensis | (75-109) | 60 | 36.7 | 0.4 |
| E. mexicana | (75-70) | 60 | 35.2 | 0.4 |
| " " | (75-74) | 60 | 36.7 | 0.4 |
| E. curvula | (75-95a) | 70 | 35.1 | 0.4 |
| E. botryodes | (75-114) | 80 | 40.0 | 0.4 |

Table 4.4 Pollen diameter (mean and standard error) of aneuploid plants of the Eragrostis species (n=50 grains)

| Species | (accession number) | 2n | $\bar{x}$(µm) | SE(µm) |
|---|---|---|---|---|
| E. heteromera | (75-170) | 41 | 30.3 | 0.3 |
| E. tenuifolia | (75-115) | 41 | 30.9 | 0.3 |
| E. atrovirens | (75-61) | 58 | 43.8 | 0.8 |
| E. chloromelas | (75-139) | ca63 | 31.1 | 0.6 |

E. chloromelas with 2n=ca.63 chromosomes was somewhat smaller (31 μm) than the pollen of the three species with 60 chromosomes (33-37 μm). On the other hand the pollen of the aneuploid E. atrovirens, with 58 chromosomes is significantly larger than that of the hexaploids (44 μm, compared with 33 to 37 μm).

## 4.4 Discussion

Although there is a very general relationship between chromosome number and pollen diameter among the taxa studied, there is too much overlap to permit the prediction of the chromosome number for a cytologically unknown species. However, the examination of pollen of a race of a species for which the pollen diameter of a known cytotype has already been determined might be a more useful indicator of chromosome number. Thus with E. cilianensis and E. minor there are very significant differences between the levels of chromosome number (Figure 4.2). However, in E. curvula this is not the case. This latter species is known to have apomictic races (Brown and Emery, 1958 and Streetman, 1963a) and the pollen of the heptaploid plants may not be fully developed. Furthermore even among related species pollen size is not an entirely reliable indicator of chromosome number though among the nine species recognised by Jones, Ponti, Tavassoli and Dixon (1978) as being morphologically most closely related to E. tef

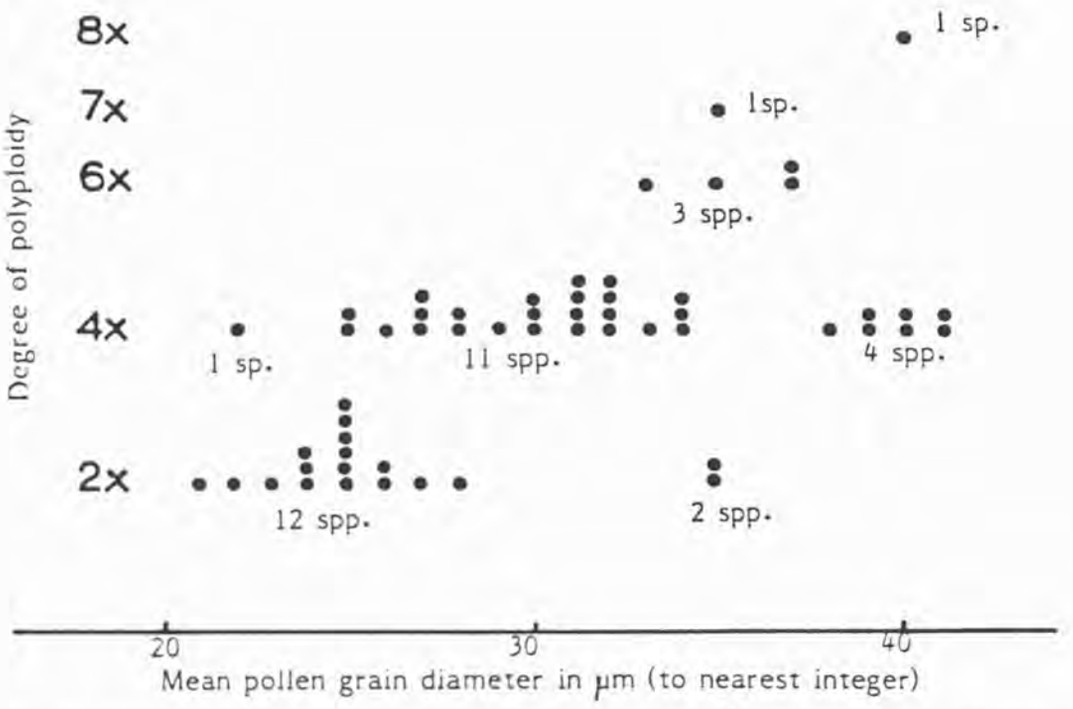



Fig. 4.1 Diagram to show the relation between the pollen-diameter and degree of polyploidy in fifty-six accessions, belonging to thirty-two species of Eragrostis (aneuploids are not included).

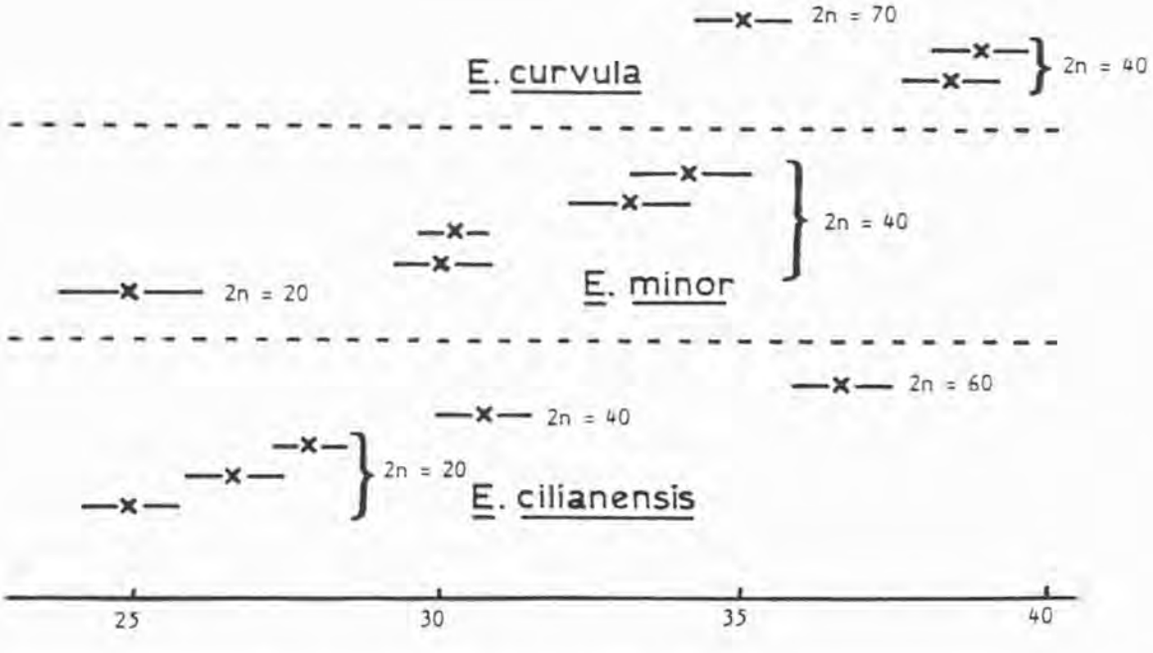



Fig 4.2 Relationship between pollen-diameter and different chromosome numbers in Eragrostis cilianensis, in E. minor and E. curvula.

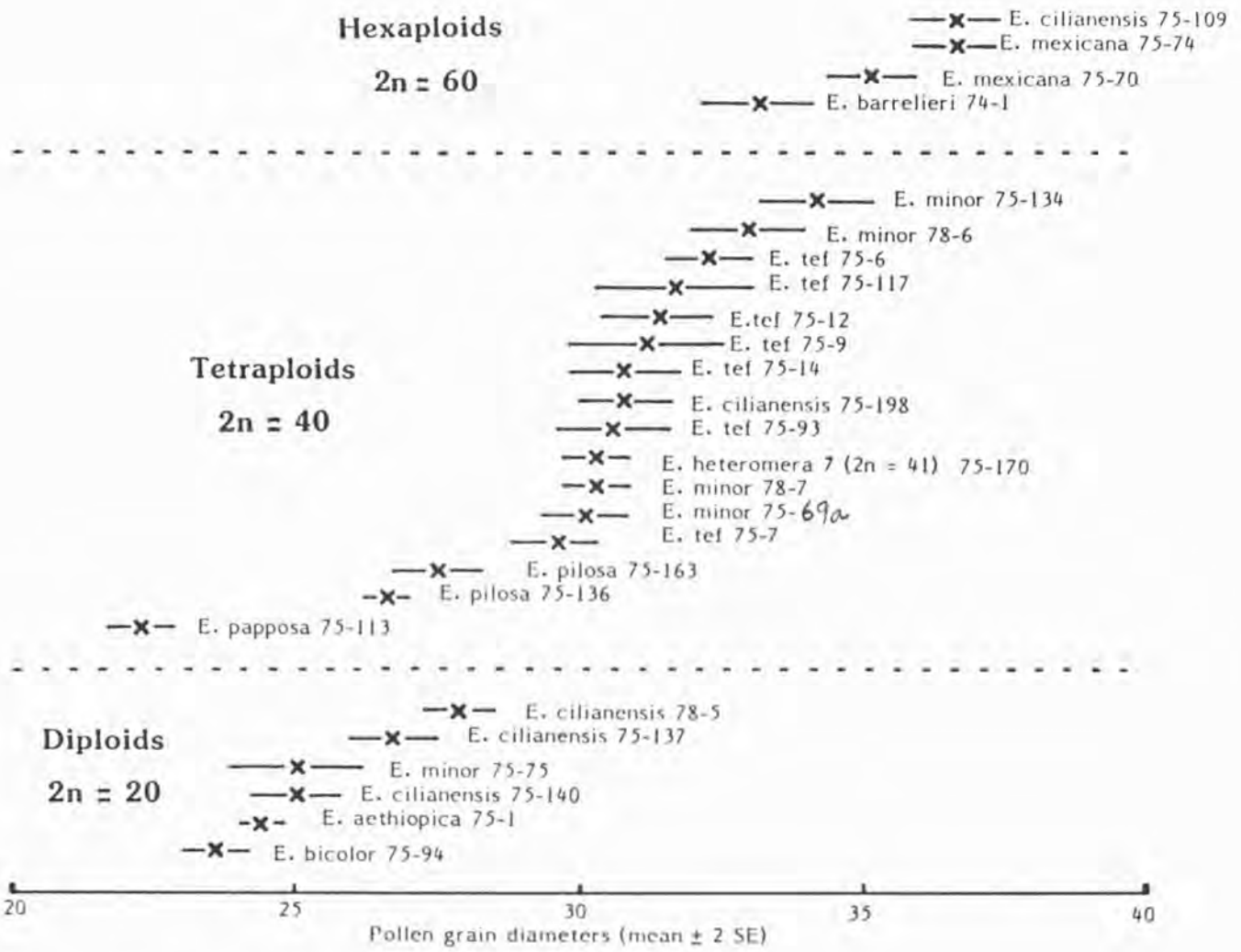



Fig. 4.3 Relationship between pollen-diameter and chromosome number among accessions of Eragrostis tef and related species.

there is better agreement of pollen size and chromosome number than within the genus as a whole (Figure 4.3). Nevertheless, even among these few species there is some overlap. E. papposa, in particular, has pollen very much smaller than one might expect, attributable (no doubt) to its irregular development (Plate 4.1). This species may be apomictic since, despite its poor pollen, it is fully seed fertile.

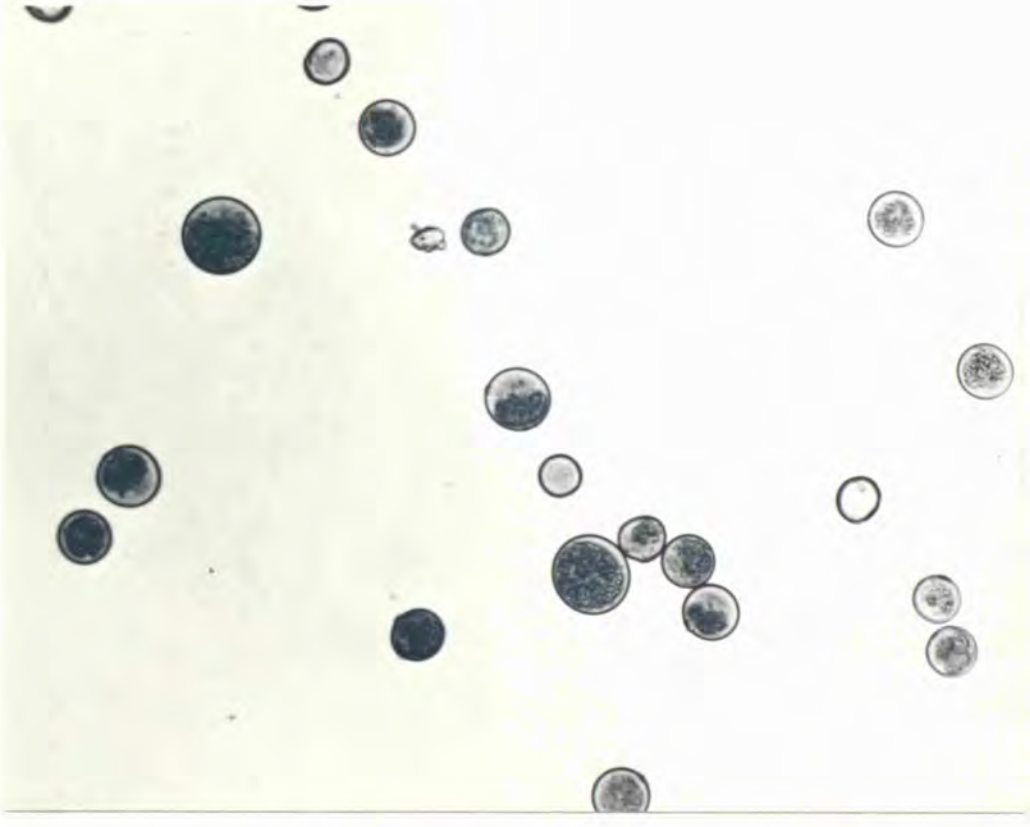


Plate 4.1 Pollen of Eragrostis papposa showing variation in size of grains and of contents. The grains which were measured were those whose densely-stained protoplast almost filled the grain (x450)

Among the tetraploid Eragrostis species an extreme of pollen size was encountered in E. superba and E. capensis, which had pollen grains as large as 40 µm in diameter. Both E. capensis and E. superba have a very distinct external morphology; they are quite unlike any other Eragrostis species studied by the present author. Ponti (1978) considered these two species as allied to Group I of her division of the genus, having some epidermal similarities with the nine other species of this group. She also mentioned that these two species are unusual in their microhairs and are completely different in caryopsis characters and in external morphology from other species she studied. Furthermore they are unique in having a relatively broad first seedling leaf.

It is interesting to compare these results with those published by other authors (Table 4.5). Pienaar (1953) found the pollen of E. plana (diploid) and its artificial autotetraploid to be 29.3 and 37.8 µm in diameter respectively. The pollen of my diploid material was 35.4 µm across, roughly the same as Pienaar's tetraploid, and having twice the volume of his diploid pollen. The remark quoted at the end of this chapter may have some bearing on differences reported by different observers for this species. The mean pollen diameter of my two tetraploid lines of E. curvula was 39 µm. Pienaar (1953) reported pollen diameters of

30.7, 31.3 and 34.3 µm from three accessions of E. curvula, all with 2n=40. Stalker and Wright (1975) reported pollen diameter of diploid E. curvula 30.2±5.2 µm, in artificially produced tetraploid 32.7±6.5 µm and in natural tetraploids 27.9±5.8 µm. The mean pollen diameter of my aneuploid line of E. chloromelas with 2n=ca.63 was 31.1 µm. Pienaar (1953) reported a diameter of 31.4 µm for an euploid plant of E. chloromelas (2n=60). He reported a pollen diameter of 33.2 µm for tetraploid E. chloromelas. It may be worth recalling that apomixis has been reported in E. curvula and in E. chloromelas (Brown and Emery, 1958 and Streatman, 1963). In my two accessions of E. pilosa the mean pollen diameters were 27 and 28 µm which closely agrees with Koch's report (1974) of a mean pollen size of 27 µm. This is reassuring and indicates that consistent measurements can be obtained by different observers on different occasions, even on plants of possibly different provenance. Jones and Newell (1948) reported the pollen diameter of the same accession E. trichodes in two successive years to be 24.5 ± 0.4 (1944) and 26.3 ± 0.4 µm (1945). Though he has not mentioned the chromosome number of this species, the somatic number so far reported for E. trichodes is 2n=40. My own measurements for known tetraploids of this species agree closely with this data (25 and 27 µm, for two accessions). The differences between

Table 4.5 Comparison between the reports of pollen diameter (μm) in Eragrostis species by different authors

| Species | Somatic Chromosome Number | Jones and Newell (1948) $\bar{x}\pm SE$ | Pienaar (1958) $\bar{x}$ | Koch (1974) $\bar{x}\pm Sd$ | Stalker and Wright (1975) $\bar{x}\pm Sd$ | Present Author $\bar{x}\pm Sd$ |
|---|---|---|---|---|---|---|
| E. curvula | 20 | | | | 30.2±5.2 | |
| | 40 | | 30.7 | | 32.7±6.5 artificial produced tetraploid | 39.0±3.2 |
| | 40 | | 31.3 | | | 38.5±2.9 |
| | 40 | | 34.3 | | 27.9±5.8 natural tetraploid | |
| | 70 | | | | | 35.1±2.8 |
| E. chloromelas | 40 | | 33.2 | | | |
| | 60 | | 31.4 | | | |
| | ca63 | | | | | 31.1±4.4 |
| E. pilosa | 40 | | | 26.6± 2.3 | | 26.6±1.8 |
| | 40 | | | | | 27.5±2.7 |
| E. plana | 20 | | 29.3 | | | 35.4±3.0 |
| | 40 | | 37.8 | | | |
| E. trichodes | ? | 24.5±0.4 (1944) | | | | |
| | ? | 26.3±0.6 (1945) | | | | |
| | 40 | | | | | 25.2±1.9 |
| | 40 | | | | | 26.7±2.7 |

observations made on the same species by different observers may reflect genetic differences due to the provenance of the plants studied, but another explanation is the effect of the environment. Jones and Newell (1948) reported some significant differences from year to year in the pollen size of some grasses even though the same stand of grass was being studied. Gould (1957) similarly found significant differences due to sampling dates in Andropogon saccharoides, and the phenomenon may be more widespread than realised. The highly significant differences among the size of pollen grains of species with the same chromosome number observed by the present author also reflect genetic differences or sampling data in some of them. For these reasons the differences observed should be interpreted with caution.

When the karyotype results are considered together with pollen volumes some interesting relationships emerge. The largest diploid pollen was found in E. racemosa, a species notable (Chapter 3) for its long and thick chromosomes. Conversely the smallest diploid pollen accured in E. gangetica a species noted for its slender and shorter chromosomes (Figure 3.1). It seems possible that the size of pollen grain may also be associated with chromosome volume, and perhaps with total DNA (though this was not measured). Certainly E. superba, with the largest pollen and with the

thickest chromosomes among the tetraploids (Figure 3.2) supports this conclusion but too few observations of karytype were made to expand the generalisation further.

# CHAPTER 5

# HYBRIDISATION

## 5.1 Introduction

There are few published reports of interspecific hybridisation within the genus Eragrostis. Hybrids have been synthesized between E. curvula x E. lehmanniana (Busey, 1976) and between E. chloromelas and E. curvula (Voigt, 1984). Unfortunately Voigt did not study the cytology of his hybrid or the parents involved. In a large genus like Eragrostis, which is taxonomically complex, the cytology and hybridisation of species can be useful in revealing the relationship between the species. Furthermore, improvement of the useful species of this genus, like E. curvula and E. tef, requires that their crossability relationships should be established.

To find out about the relationship between E. tef and its closely related species, the present author attempted (in 1978-79) to cross some of the annual species considered to be related to E. tef (Jones et al., 1978) and also to cross E. tef with these species.

Although it has been known for some time that E. tef reproduced sexually (Melak and Guard, 1966), all attempts to cross lines of t'ef failed up to 1974 (Tareke, 1981) because of the lack of knowledge of the floral biology of this species. E. tef was assumed to be cleistogamous (Melak and Guard, 1966) until the report of chasmogamy by Tareke (1976). Tareke noticed that t'ef flowered very early in the day (6.45am - 7.45am in Ethiopia) and found that anthesis was of very short duration even for a grass. Before that observation, t'ef improvement was carried out only by mass selection from the extensive variation in cultivation. This diversity is considerable and Bekele (verbal communication), on the basis of biochemical studies of different varieties of E. tef, has suggested the possibility that some of the varieties of E. tef in fact are different species. However, Tareke (1976, 1981) and Ponti (1978) have managed to obtain fertile hybrids between different varieties of E. tef. Successful attempts were made by the present author to cross two extreme types of t'ef (in 1978). The results of my hybridisation experiments and observations of meiosis in the synthesised hybrids are reported in this chapter.

5.2 Method

The plants which were chosen to be crossed were kept in the dark in a cold room at 10°C from between 5.30 and 6.00pm the day before the crosses were to be made until 8.30am the following morning. This delayed the opening of the flowers, which would otherwise have begun to open at dawn. Since anthesis in E. tef and its relations is rapid (5 to 30 minutes, Ponti, 1978) hand-pollination has to be performed rapidly. Therefore very few crosses could be done in a day (Tareke, after several years experience reported (1981) a maximum of three). This is the procedure followed when making a cross:

1- The plant which was going to be used as the male parent was brought out of the cold room and as the flowers opened the anthers were removed with fine forceps. Because of the small size of the flowers this was done at a magnification x40 under the binocular microscope, while the plant was lying on its side on the table.

2- The anthers were than put on a glass slide lying on damp filter paper in a Petri dish.

3- The plant which was going to be used as the female parent was taken out of the cold room and as a flower opened its indehised anthers were removed with the fine

forceps (If the anther seemed aberrant but the stigma was receptive the anthers were not removed).

4- The lid was removed from the Petri dish and an anther removed with forceps. If the anther had already dehisced, pollen was applied to the stigma; otherwise the anther was gently squeezed as it was brought into contact with the stigma.

5- The spikelets below and above the spikelet carrying the crossed flower were cut off and a label describing the position of the treated floret in the spikelet and the position of the branchlet itself was attached to the panicle.

Seeds, if formed, were germinated on a damp filter paper in a Petri dish before transplanting to a pot. The F1 was grown in the glass house and examined to confirm its hybrid status. After self-pollination, F2 seed was collected. Fifty seeds of the F2 progeny of each of the dubious crosses, between E. tef x E. tef (75-12 x 75-6) and E. tef x E. cilianensis (75-12 x 75-168), were grown under glass. About two hundred plants of the F2 generation of genuine crosses between E. tef x E. tef (75-12 x 75-7) were grown outdoor in Botanical Supply Unit in Egham, England. Segregation was observed in these F2 to confirm the hybrid nature of the F1.

Among the plants which were grown it was noticed that some plants of an accession of E. minor (75-88) produced few seeds (see Chapter 2). Nevertheless the plants opened their flowers normally and their stigmas seemed receptive. Because of their male-sterility, some of the plants were used as a female parent for hybridisation.

Meiosis of the hybrid between two varieties of E. tef (75-12 x 75-7) and meiosis of the hybrid between E. minor (75-88) and E. cilianensis (75-168) were studied, using the method as described in Chapter 2. The somatic chromosome number of the hybrid E. minor x E. cilianensis was determined as described in Chapter 2.

## 5.3 Results

Table 5.1 shows the results of seventy-seven crosses made by the present author involving eight species combinations. Crosses following emasculation were less successful (4 grains from 59 pollinations) than those made with the male-sterile (MS) lines of E. minor and E. tef (5 grains from 17 pollinations). Emasculated flowers gave seed only from three of seven parental combinations. One was a cross between two chromosome races of E. cilianensis, with the diploid as the recipient of pollen from the tetraploid parent. This cross produced two shrivelled grains (Plate 5.1)

Table 5.1 Hybridisation attempted between and within Eragrostis species

| Parents | Emasculate or male-sterile | Number of Pollinations made | Grains formed | Grains germinated | Morphology of F1 |
|---|---|---|---|---|---|
| E. tef (4x) X E. tef (4x) | | | | | |
| 75-12 X 75-7 | MS | 1 | 1, normal | | Mainly parental |
| 75-12 X 75-7 | E | 2 | 0 | - | - |
| 75-12 X 75-6 | E | 3 | 1, normal | | Maternal |
| 75-6 X 75-12 | E | 2 | 0 | - | - |
| E. tef (4x) X E. cilianensis (4x) | | | | | |
| 75-12 X 75-168 | E | 7 | 1, normal* | | - |
| 75-12 X 75-168 | MS | 1 | 1 | | Maternal |
| E. tef (4x) X E. pilosa (4x) | | | | | |
| 75-12 X 75-136 | E | 15 | 0 | - | — |
| 75-7 X 75-136 | E | 5 | 0 | - | — |
| 75-12 X 163 | E | 4 | 0 | - | — |
| 75-12 X 75-163 | MS | 4 | 0 | - | — |
| E. minor (4x) X E. tef (4x) | | | | | |
| 75-88 X 75-12 | MS | 5 | 1, shriveled | 0 | - |
| 75-88 X 75-7 | MS | 3 | 0 | - | - |

| | | | | | |
|---|---|---|---|---|---|
| E. cilianensis X E. cilianensis | | | | | |
| 75-140 (2x) X 75-168 (4x) | E | 5 | 2, shriveled | 0 | - |
| 75-168 (4x) X 75-140 (2x) | E | 2 | 0 | - | - |
| 75-168 (4x) X 75-109 (6x) | E | 2 | 0 | - | - |
| 75-109 (6x) X 75-168 (4x) | E | 4 | 0 | - | - |
| E. minor (4x) X E. cilianensis (4x) | | | | | |
| 75-88 X 75-168 | MS | 3 | 2, normal | 2 | Intermediate between parents, sterile |
| 75-134 X 75-168 | E | 2 | 0 | - | - |
| E. mexicana (6x) X E. cilianensis (6x) | | | | | |
| 75-70 X 75-109 | E | 3 | 0 | - | - |
| E. barrelieri (6x) X E. mexicana (6x) | | | | | |
| 74-1 X 75 -70 | E | 4 | 0 | - | - |

* Grain lost. As Tareke comments (1981,p.20) "The tiny seeds of tef demand very careful handling"

from 5 pollinations, the three reciprocal pollinations being unsuccessful. The other was a cross between E. tef and E. cilianensis, the grain of which was produced last. The third one was a grain produced after a cross between two t'ef varieties which grew into a plant with maternal characteristics, as did the selfed F2. This grain was apparently the result of accidental self-pollination, or possibly of agamospermy, which is known to occur in other species of the genus.

Plate 5.1

Inviable grains produced by crossing E. cilianensis 2x x 4x (left); normal selfed 2x grain for comparison (right). (all x70)

The MS flowers gave seed from four of five parental combinations. One, a cross between two tetraploids, E. minor and E. tef, gave one shrivelled grain from 5

pollinations. The other three combinations produced four normal grains. One developed after an attempt to cross E. tef and E. cilianensis; when this seed was grown the F1 plant had all maternal characters. The F2 were also uniformly maternal. Two seeds were formed as a result of crossing between tetraploid E. minor x tetraploid E. cilianensis. These two seeds were grown and the F1 plants were both alike and sterile. Their morphology was intermediate between the two parents, but closer to the maternal one, E. minor (Plate 5.2) The spikelet of E. minor is narrower (1.25-1.75mm) than that of E. cilianensis (2-2.25mm). The width of the spikelet of the hybrid varied considerably according to the spacing of the flowers, but mostly was about 1.75mm. The length of the spikelet was not a good indication because it varied from 5 to 13mm in the hybrid. The size and width of the lemmas, but not the glumes, was also intermediate between the two parents. The leaf of the hybrid was narrower than that of the male parent.

The other seed was formed as a result of crossing two varieties of E. tef, produced an F1 which was obviously a hybrid (Plate 5.3 and 5.4). It had the lax panicle and brown seeds of its male parent (the panicle was compact and seeds were white in the female parent), but the lemmas were dark purple. The lemma colour in the male parent was red and in the female it was greenish with pink tip. The F2 generation showed a segregation

PLATE 5.2 Hybridisation of Eragrostis minor (2n=40) and Eragrostis cilianensis (2n=40).

Top left: E. minor 75- 88; Female parent.

Top right: E. cilianensis 75-168; Male parent.

Bottom left: Synthetic hybrid. (all the plants are X 0.1).

Bottom right: Part of the Panicles of E. minor (left), the hybrid (centre) and E. cilianensis (right) X 1.25.

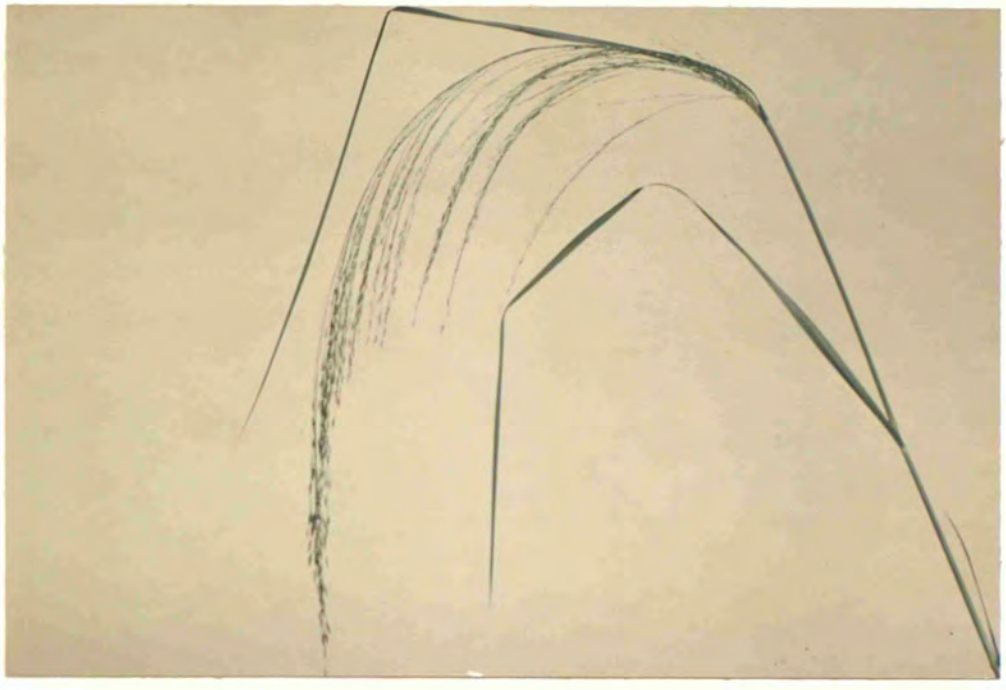


PLATE 5.3 Panicles of the parents of a tef-tef hybrid, X 0.4
Top: 75-7 greenish, loose panicled type used as male parent.
Bottom: 75-12 red, compact panicled type used as female parent.

PLATE 5.4 Panicles of $F_1$ plant (Top X 0.4) and a selection of $F_2$ generation (Bottom X 0.25), of the intervarietal hybrid 75-12 X 75-7 in Eragrostis tef. The $F_1$ is uniformly purple and loose-panicled; the $F_2$ shows segregation of the genes determining these characters.

of panicle type and lemma colours (Plate 5.4)

Meiosis in the Hybrids

Meiosis in the hybrid between two varieties of E. tef was normal, with 20 bivalents at metaphase I (Plate 5.5). Anaphase I was normal in this hybrid too.

Somatic chromosome number in the hybrid between tetraploid E. minor (2n=40) and E. cilianensis (2n=40) was, as it was expected to be, 2n=40 (Plate 5.5). Meiosis in this hybrid was abnormal (Plate 5.5). Fourteen of the pollen mother cells studied at diakinesis and metaphase I had roughly equal numbers of bivalents and univalents: in several of them thirteen bivalents and fourteen univalents were clearly visible. Up to eleven laggards were observed at anaphase I of this hybrid and at metaphase II variable numbers of chromosomes were observed which were not located on the metaphase plate.

## 5.4 Discussion

Crossing the small flowers of Eragrostis species (they are less than 4mm long) is difficult and a fair amount of practice is needed to perfect the technique. Not only is considerable manipulative skill required but the timing of the operation is crucial if selfing is to be avoided. The negative results for many of the

PLATE 5.5 Chromosome divisions of synthetic Eragrostis hybrids.

A. only E. tef 75-12 x E. tef 75-7.

A. Meiosis: normal diakinesis with 20 bivalents X 2200.

B-E E. minor 75-88 x E. cilianensis 75-168.

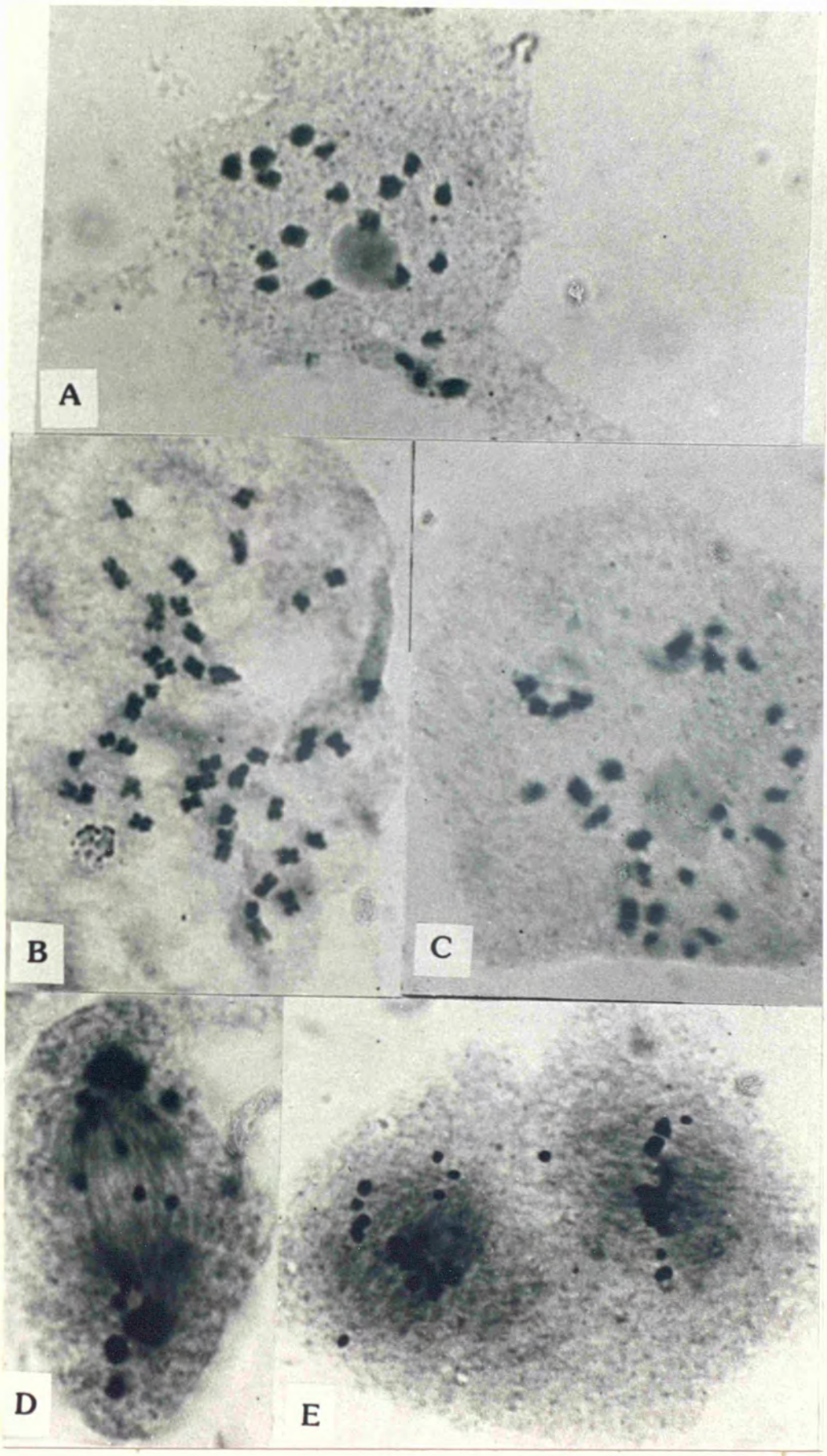
B = Root tip mitosis C-E = Meioses (All X2200).

B. Metaphase with 2n = 40.

C. Diakinesis with roughly equal numbers of bivalents and univalents.

D. Anaphase I with laggards.

E. Metaphase II showing many chromosomes not localised in equatorial plate.


A
B
C
D
E

crosses attempted must by interpreted with caution; greater experience and larger numbers of pollinations may have allowed many more hybrids to be synthesized. Even so, few hybrids were produced from a significant expenditure of effort. Nature, on the other hand, has time and numbers on her side; therefore hybrids may be expected to occur from time to time where taxa flower together. The observation of a natural hybrid between t'ef varieties in a seed sample of one variety (Ponti, 1978) confirms this, as does the occurrence of an interspecific hybrid in a batch of seed of E. minor which I grew from a Botanic Garden source (see later in this Chapter).

Natural hybridisation is important in providing the diversity found within t'ef. Mutations occur from time to time and occasional crossing creates new combinations of characters. One such mutation was observed in the course of this study. One branch of a plant with red lemmas (line 75-12) produced a single shoot with yellowish-white lemmas (Plate 5.6).

Plate 5.6 Somatic mutations in Eragrostis tef 75-12.

Left: a plant of the 'red-foxtail' type has produced a yellowish-white panicle (x1/5). Right: the shoots are separated by hand to show that a single shoot bears both red and yellowish-white panicles (x1/10).

The higher success rate of crosses using the two male-sterile plants further confirms that hybridisation may occur more readily than the results of crossing after emasculation might suggest. Three interspecific

hybrids were synthesised, using a MS parent, which were not produced by crossing after emasculation; that the emasculation process may result in physiological disturbance was once suggested by Tareke and Miller (1976), to explain the low success-rate of t'ef-t'ef crosses. Several workers have therefore attempted to induce MS by applying gametocides but with only limited success (Tareke and Miller, 1978; the present author, work done in 1978; and Seyfu, 1983).

The occurrence of two maternals in the progeny of crosses is most readily explained by accidental selfing, especially as the risks of pollen contamination are high due to synchronous flowering. Nevertheless the possibility of facultative agamospermy cannot be ruled out; it is known to occur in several other Eragrostis species: E. curvula, E. heteromera and E. chloromelas (Brown and Emery, 1958); E. curvula, E. chloromelas and E. lehmanniana (Streetman, 1963a).

The normality of meiosis in the hybrid between two such distinct varieties of E. tef (75-12 x 75-7), and also the fertility of the hybrids between different varieties of E. tef made by Tareke (1976, 1981), Ponti (1978) and Seyfu (1983) indicate against Bekele's suggestion that different varieties of E. tef could, in reality, actually be different species.

The segregation of lemma colour and panicle type in the F2 hybrids followed the pattern reported by Tareke (1981).

The dominance of brown grain colour (over white) and loose panicle (over compact) in the F1 hybrid between the two varieties of E. tef (75-12 x 75-7) is also in agreement with the conclusions of Tareke (1976 and 1981) and Ponti (1978).

Meiosis in the synthesised hybrid between the tetraploids E. minor and E. cilianensis was similar to the meiotic behaviour of the sterile plant I noted in a batch of the seed of E. minor (75-69) (Chapter 2). The morphology of these two plants was also very similar (Plate 5.7).

Plate 5.7

Spikelets from the putative natural (left) and synthetic (right) tetraploid hybrids of Eragrostis minor x E. cilianensis (x7). The specimens were taken at random and the numbers of florets, 20 left, 18 right, vary considerably in the material.

For these reasons it seems probable that 'sterile E. minor' is a natural hybrid which has happened in a Botanic Garden. Such hybridisation may explain the variation which occurs in some Eragrostis species, with attendant difficulties of identification. Both E. minor and E. cilianensis are polymorphic species as well as being very similar to each other. Dr. Clayton (personal communication) agrees that it can be difficult to assign a specimen to one or other species. Yet, from the evidence here presented it would appear that there are major barriers to gene-exchange both between and within E. minor and E. cilianensis.

The shrivelled seeds which were obtained as a result of crossing diploid and tetraploid E. cilianensis may be the result of "seed-incompatibility", where the disturbance of the normal polyploid relationship between the embryo and the endosperm tissue leads to a collapse of the endosperm (Stebbins, 1980). There was no such disturbance in the crosses between the tetraploid E. minor and E. cilianensis. The same explanation cannot be applied to the failure of the development of the hybrid embryos formed by crossing the two tetraploid species E. minor x E. tef, where gene-antagonism may be invoked as an explanation.

The demonstration of a barrier to gene exchange within the E. cilianensis complex has evolutionary implications: the different chromosome races are on the way to becoming distinct species. In the case of the barrier between E. minor and E. tef, it is of more than academic importance for it prevents the ready transfer of genes into the cereal. It may be possible to raise the embryo (by excission and growth on sterile media, as has been done for Trifolium pratense x repens (Evans, 1962), but this will be a further complication to an already exacting procedure for the improvement of t'ef. It would seem more appropriate to direct breeding effort to an utilization of the extensive gene pool of t'ef (over a thousand lines are maintained inthe Addis Ababa gene bank according to Seyfu, 1983), rather than attempting introgression from related species.

The regular observation of thirteen bivalents and fourteen univalent chromosomes in the first division of meiosis in the hybrid between tetraploids E. minor and E. cilianensis (Plate 5.5) indicates the homology (or homeology) of more than two genomes in the hybrid. An explanation is required for the formation of thirteen rather than ten or twenty bivalents: it may be due to autosyndetic pairing in addition to ten bivalents formed from a genome common to both species.

Clearly these studies, together with those of Busey (1976) and Voigt (1984) on the closely related species E. curvula, E. chloromelas and E. lehmanniana do no more than scratch the surface of the cytogenetics of this large and complex genus.

# CHAPTER 6

# GENERAL DISCUSSION

## 6.1 Eragrostis

Hartley and Slater (1960) who studied the distribution of the subfamily of Eragrostoideae, concluded that the subtribe Eragrostinae originated from Africa and "showed many characters regarded as primitive in the grass family" (although they do not list them). The symmetrical chromosomes of Eragrostis (Chapter 3) confirm its primitive status on Stebbins' (1971) conclusion that "in the plant kingdom as a whole, symmetrical karyotypes are usually primitive", whereas asymmetry is usually a derived state.

The chromosome morphology among the Eragrostis species studied did not show very great differences between species, but some species (E. namaquensis var. diplachnoides, E. superba) were sufficiently distinct for me to believe that karyotype will be a useful source of taxonomic information; in particular E. namaquensis var. diplachnoides stands apart from other studied species of the genus (Chapter 3). A wider study of karyotypes in the genus (only sixteen species have so far been stuied) would be an important step in

the recognition of subgenera, sections and series within the large genus Eragrostis.

Chromosome numbers are far from constant in Eragrostis species. Among the fourteen species for which I had more than one accession, three of them had two and one (E. cilianensis) had three chromosome races. I also found aneuploid plants in four species (Chapter 2). The published data for the genus (including my contributions) shows that 35 of the 120 species for which counts are reported have two or more chromosome races. Bearing in mind that 45 species have only been cytologically examined once, it would appear that inter-specific chromosomal variation is common, because nearly half the remaining species have two or more reported chromosome races. Even when allowance has been made for the possibility of misidentification of some of the plants, whereby new counts are credited to the wrong species, it seems that Eragrostis is a genus with a high degree of chromosomal diversity at the level of species. This, in turn, indicates that evolution has been recently proceeding rapidly within species and this is confirmed by the taxonomic difficulties which are widespread in Eragrostis. Some of these taxonomic problems may be directly ascribed to polyploidy itself, and especially allopolyploidy, which obscures the distinctions between species by giving rise to species combining the characteristics of two progenitors.

Stebbins (1956) mentioned that the difficulty in delimiting species of grasses is because of the hybridisation and chromosome doubling which has blurred the interspecific boundaries. Unfortunately there are only two reports of interspecific hybridisation in Eragrostis (Voigt, 1984 and Busey, 1976) and neither occurred naturally. Voigt obtained a hybrid between E. curvula and E. chloromelas, but did not study the cytology of the hybrid or the parents. Busey made a hybrid between E. lehmanniana (2n=60) and E. curvula (2n=40) by enclosing an inflorescence of each in a bag. The hybrid combined characteristics of both parents, had fifty chromosomes and a highly irregular meiosis with mostly bivalents, some univalents and relatively few multivalents.

The present author's sterile hybrids between E. minor x E. cilianensis indicate that it is easy to make hybrids if the circumstances are favourable: a male-sterile plant as pollen recipient, manipulative dexterity on the part of the operator and parents with the same chromosome number. It is extremely desirable that more hybrid Eragrostis should be synthesized and studied cytologically since this would help to establish the relationships of species and to permit their phylogenies to be worked out.

The high proportion of species with two or more chromosome races (about one third of all those which have been cytologically examined) raises another issue: are these species really species aggregates, containing recognizable but only slightly different species with different chromosome numbers, or are they species containing indistinguishable chromosomal races? Løve (1951) indicates that all polyplotypes (the term he uses for chromosome races) should be classified as distinct species. He says that this principle should only refer to sexual species and not to asexually reproducing types with odd multiples of chromosome base number. He also asserts that there are always some morphological differences between polyplotypes.

There were four Eragrostis species which I found had more than one chromosome race in my material. E. curvula had 2n=40 and 2n=70; the latter race having an odd multiple of the base number and reproducing apomictically (Brown and Emery, 1958, Streetman, 1963a) is still part of E. curvula even on Løve's criteria. The other three species are more problematical: E. cilianensis showed some morphological differences between the plants with 2n=20, 40, 60 (Plates 6.1 and 6.2); for example the two accessions with 2n=20 were shorter than those with 2n=40 and 2n=60. The accession with 2n=40 was somewhat taller and had its panicle more open and longer than those with 2n=20 and 60. The two

PLATE 6.1 Morphology of four races of *Eragrostis cilianensis*, (all X 0.15).

| | | | |
|---|---|---|---|
| Top left: | 75 - 137 | 2n=20 | Portugal. |
| Top Right: | 75 - 140 | 2n=20 | Unknown origin. |
| Centre: | 75 - 168 | 2n=40 | Mozambique. |
| Bottom: | 75 - 109 | 2n=60 | Ethiopia. |

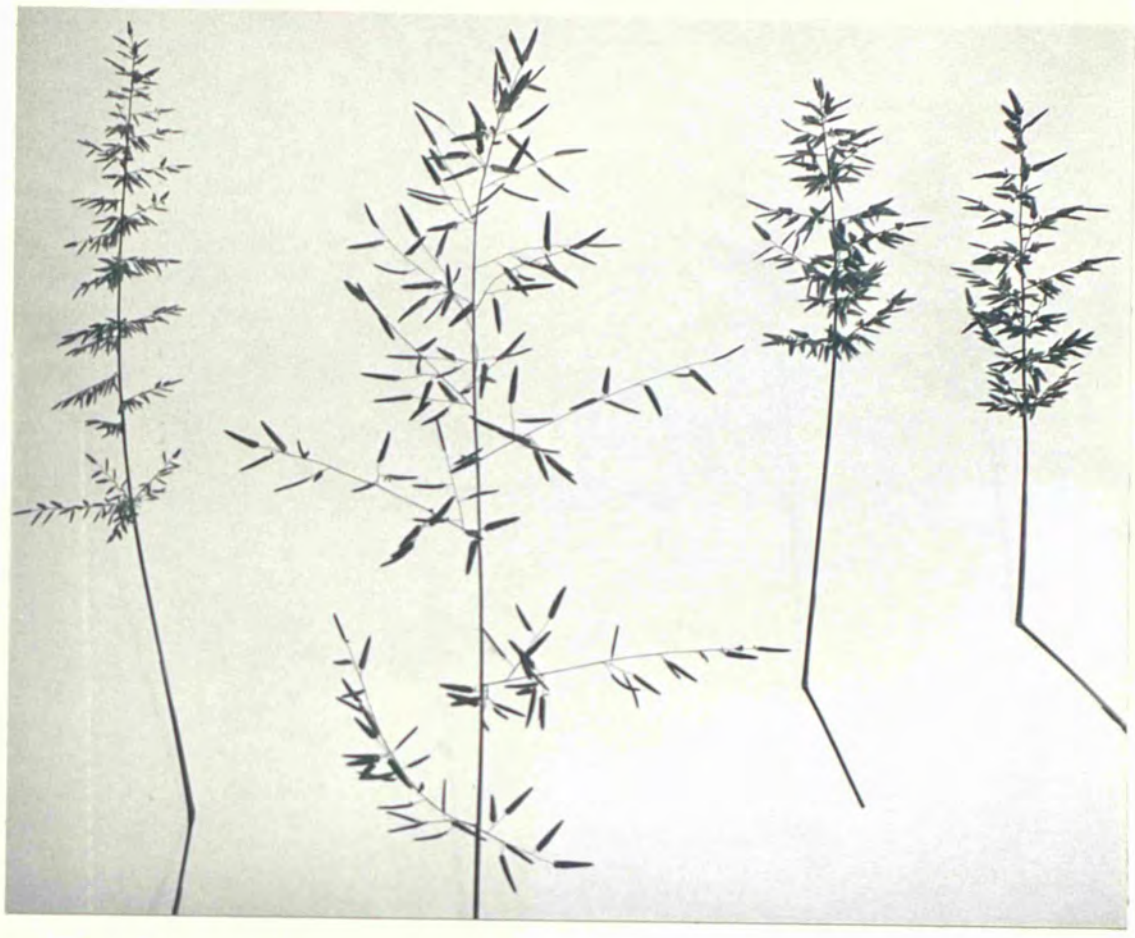
PLATE 6.2

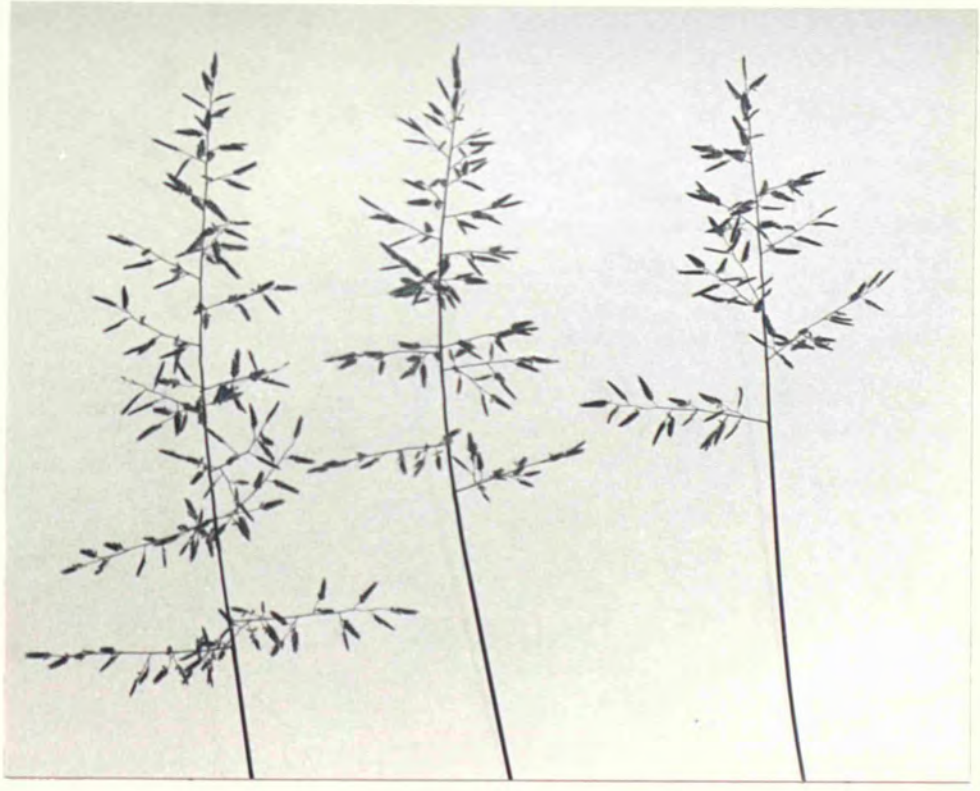
Top: Panicles of the four plants of Eragrostis cilianensis figured in Plate 6.1.

Right to left: diploid (75-137), diploid (75-140), tetraploid (75-168), hexaploid (75-109) X 0.4.

Bottom: Panicles of the three plants of Eragrostis minor figured in Plate 6.3.

Right to left: diploid 75-75), tetraploid (75-134), tetraploid (75-69a) X 0.6.





dipoid accessions had a shorter panicle than the plant with 2n=60. The leaf was longer and wider in plants with 2n=40 than those with 2n=60 and 20. It should be mentioned that the size of plant and even panicle varies in different environments and even at times on the same plant. For example Ponti (1978) has mentioned a very congested panicle and a moderately congested one on the same plant of one accession of E. cilianensis. It is worth recording that the size of the lemma, glumes, paleae and grains were similar for all accessions of E. cilianensis studied. Thus it cannot be denied that morphological differences occurred between the three chromosome races I studied, but they are small and would be difficult to observe in a herbarium specimen. Furthermore, even a casual glance at herbarium material reveals that there is much more variability within E. cilianensis as a whole than occurs in my material and one does not know how much of it is determined by the environment. There is not a clear case that Løve's principle is at work.

In Eragrostis minor differences in plant size were observed even among different accessions having the same chromosome number (Plates 6.2 and 6.3). One accession with 2n=40 was much shorter than the two other accessions, one of which also had 2n=40 while the other had 2n=20. The diploid and one of the tetraploids (shorter one) had panicle nearly similar in size, while

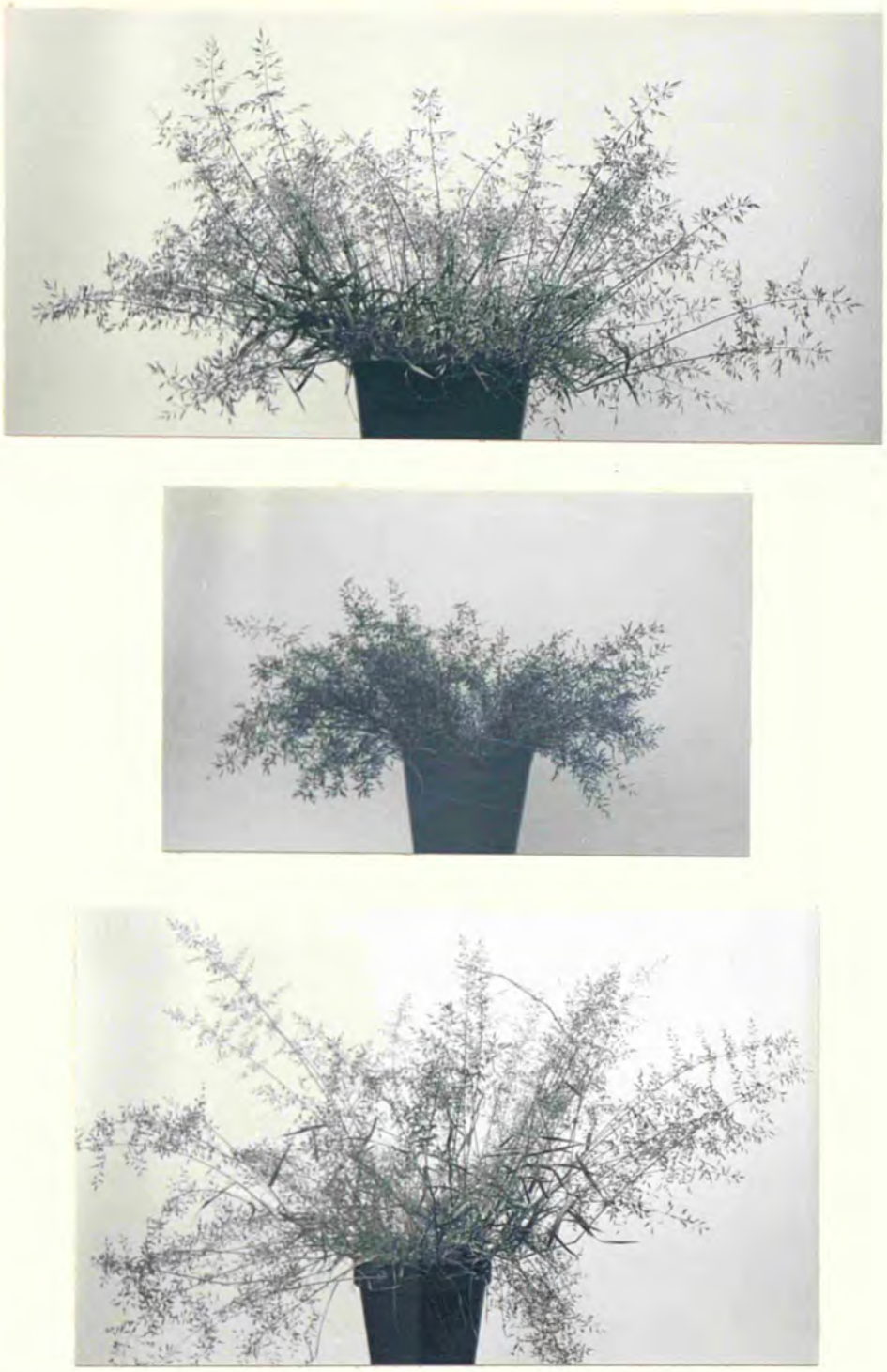


PLATE 6.3 Morphology of three races of Eragrostis minor

all X 0.15.

Top: 75-75 2n = 20 unknown origin.

Centre: 75-134 2n = 40 France.

Bottom: 75-69a 2n = 40 ? Usbekistan.

the other tetraploid accession had a larger panicle than them. The size of lemma, palea and glumes were similar in all three accessions. As far as E. pectinacea with 2n=40 and 2n=60, the two plants were closely similar in appearance, having only very small differences in the size of floral parts (the hexaploid being a little larger).

Clayton (personal communication) says that there is a lot of variation within both E. cilianensis and E. minor and much of it cannot be attributed to differences in chromosome number. He has not found it possible to recognise entities within these species which might correspond to my chromosome races and he therefore does not think that these chromosome races merit taxonomic recognition, and once again Løve's principle does not hold.

It would be appropriate to examine a larger sample of all these widespread species to test these conclusions. It may yet prove possible to recognise 'marker characters' in such variable species which are correlated with chromosome number; they should then be treated as species-complexes.

However, Leigh (1980) who determined the chromosome number in E. curvula complex (including E. chloromelas), commented "Although these data are only fragmentary, and further studies are necessary before definite

conclusions can be drawn, nevertheless it would seem that the different types are characterised by different chromosome number; for example his material of E. curvula had 2n=ca.40 and his E. chloromelas had 2n=ca.60. Appendix 1 shows that his conclusion is reasonable as thirteen counts out of seventeen for E. chloromelas are between 2n=60 and 2n=63 (including my observations) and only one is 2n=40. On the other hand, E. curvula had numbers ranging from 2n=20 to 2n=80 with 2n=40 being predominant. It is worth noting that Clayton (1974) considers E. chloromelas to be synonymous with E. curvula, but I have chosen to follow Gould (1968) in treating them as specifically distinct species.

## 6.2 Polyploidy

A sufficient number of species of Eragrostis have now been examined to allow us to draw some preliminary conclusions about the frequency of polyploidy in the genus. The percentage of polyploidy has been considered to be lowest in warm climates and highest in polar ones (Reese, 1958). If this generalization held true in the grass family, we might expect a high percentage of polyploidy among Pooid grasses and a low percentage among Eragrostoid grasses. The genus Eragrostis does not support this view, perhaps because the Eragrostoideae have undergone variative evolution

since the Oligocene (Hartley and Slater, 1960). In their case, it was in response to the development of desert areas, in the case of temperate grasses it was in response to polar fluctuations.

The tetraploids are the most frequent level of polyploid, being nearly twice as numerous (40%) as the diploids (24%) and slightly more numerous than all the higher polyploids put together. Stebbins (1971) has termed this type of structure a "mature polyploid complex".

Favarger (1967) regards a high proportion of tetraploids, associated with surviving diploids and without a large superstructure of higher polyploids, as evidence of recent evolution; on this interpretation Eragrostis has many neopolyploid species and races.

These two views are equally valid because evolution must have been proceeding for sometime to give so many polyploids in the genus, but the excess of tetraploids coupled with much taxonomic complexity indicate that there has been a recent cycle of tetraploids from the diploid level to distort what would otherwise be a pyramidal structure of chromosome frequencies.

The genus Eragrostis has an honoured place in the study of polyploidy. It was Hagerup's comments upon the chromosome numbers of three species of Eragrostis

growing near Timbuktu in the Southern Sahara which began the once widely accepted idea that polyploids are tougher, more vigorous species capable of tolerating extreme environmental conditions - hence their later association with mountains, polar climates, continental climates and saline environments (reviewed in Stebbins, 1950 and 1971). Hagerup (1932) observed that a small, ephemeral Eragrostis species growing in standing water at the foot of the dunes was diploid; the larger perennial species on the drier sides of the dunes was tetraploid and the most robust species from the exposed tops of the dunes was an octoploid. This kind of relationship does not hold for the genus as a whole. Some perennials are diploid, many polyploids are ephemerals. The higher polyploids are not necessarily plants of hostile environments. Stebbins (1947) commented: "the example of Eragrostis, first given by Hagerup (1932) and widely cited in general references as an example of the effect of autopolyploidy, is particularly doubtful. Eragrostis is a very large and complex genus, in which good taxonomic characters for separating species are particularly hard to find. Furthermore, it is very poorly known cytologically. Hence, until more is known about the cytology of other African desert species of this genus, the status of the three cited by Hagerup must be considered ambiguous". It is worth noting that Hagerup at that time did not

distinguish between auto- and allo- polyploidy, so Stebbins, like others, seems determined to read more than Hagerup actually wrote. Stebbins' comments on the taxonomy and cytology are more pertinent, however.

There is some geographical variation in the distributions of the chromosome races of Eragrostis but nothing to support the generalizations which others have drawn from Hagerup's observations.

## 6.3 T'ef

The demonstration that several species have karyotypes similar to that of t'ef has implications for the improvement of this cereal. These species were all among the nine species previously considered, on morphological grounds, to be related to t'ef (Jones, Ponti, Tavassoli and Dixon, 1978). The newer cytological evidence, together with the evidence of Ponti (1978), allows us to shorten the list of closely related species to six, three of which have not been karyotyped (marked with an asterisk in the list below). These species are

E. aethiopica 2x

E. pilosa 2x

E. mexicana 6x

*E. barrelieri 6x

*E. minor 2x,4x

*E. cilianensis 2x,4x,6x

The three excluded species are all perennials: E. bicolor has a different karyotype to t'ef; E. heteromera has a rather less different karyotype; E. papposa has not been karyotyped.

The synthesis of the first hybrid between t'ef and another species will be an important step in the potential improvement of the crop species. Unfortunately it was not possible to make hybrids between t'ef and its three tetraploid relatives -- the facility with which the tetraploid lines of E. minor and E. cilianensis could be crossed gives some encouragement here. But, since there is so much variation within t'ef itself, it seems best to identify useful genotypes within the species and to combine their genes by crossing.

The demonstration that the seven lines of t'ef, selected to represent some of the more extreme types found in the species, were all tetraploid is also interesting. A large sample would have to be examined to be certain, but it seems possible that the species is tetraploid throughout; if other chromosome races occurred in it, I would probably have found one in my sample. In turn this focuses our attention on E. cilianensis, E. minor and E. pilosa as possible donors of genomes to E. tef since, with its regular

meiosis (Chapter 2) and high fertility, it is likely to be of allopolyploid origin. It is interesting to note that Hackel (1887), who wrote the account of grasses in Die naturlichen Pflanzenfamilien, considered t'ef to be a cultivated type of E. pilosa; Ponti (1978) also considered E. pilosa to be the wild species nearest to t'ef.

Acknowledgements

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Appendix 1: Reported Chromosome numbers of

*Eragrostis* species

| Species | n | 2n | Author | Locality |
|---|---|---|---|---|
| E. aethiopica Chiov. | 10 | 20 | Jones, Ponti, Tavassoli and Dixon (1978) | South Africa, Transvaal, Shingwidzi |
| E. acutiflora (H.B.K.)Nees | 20 | | Gould and Soderstrom (1970a) | Mexico, Oaxaca |
| | 20 | | Davidse and Pohl (1974) | Venezuela, Guarico, Calaboso |
| E. airoides Nees | 36 | | Davidse and Pohl (1974) | Venezuela, Distrito Federalo, Carayaca |
| E. albida Hitchc. | 20 | | Hagerup (1932) | Africa, Mali, Timbouctou |
| E. annulata Rendle | | 20 | Nordenstam (1969) | Namibia, Omaruru Distr., Brandberg |
| E. aquatica Honda | | 60 | Tateoka (1967) | Japan, Seika-Cho, Kyoto Pref |
| E. aspera (Jacq.) Nees | | 20 | Avdulov (1931) | ? |
| | | 20 | Moffett and Hurcombe (1949) | Zimbabwe |
| | | 20 | Moffett and Hurcombe (1949) | South Africa, Cape Prov., Kimberley |

| | | | | |
|---|---|---|---|---|
| | | 20 | A.T. unpublished | Zimbabwe, Manicaland, Umtali, Uumba |
| E. atherstonei Stapf | | 40 | Moffett and Hurcombe (1949) | South Africa, Cape Prov., Mafeking |
| | | 40 | Moffett and Hurcombe (1949) | South Africa, Cape Prov., Mafeking |
| | | 40 | Pienaar (1955) | South Africa, Distr. Pretoria |
| E. atrovirens (Desf.)Steud. | | 40 | de Wet (1960) | South Africa |
| | | 60 | Larsen (1963) | Thailand, Payap, Doi Intanon |
| | | 60 | Larsen (1963) | Thailand, Payap, Doi Saket, East of Chiengmai |
| | 10 | | Kammacher, Anoma, Adjanohoun and Aké Assi (1973) | Ivory Coast, Road to Toupe |
| | | 60 | Christopher and Abraham (1974) | South India, Mahendragiri |
| | 30 | | Gould and Soderstrom (1974) | Ceylon, North Central Province |
| | 30 | | Gould and Soderstrom (1974) | Ceylon Western Province |
| | | 60 | Dujardin (1978) | Zaire, Bandundu, Suka, South East of Kasango |

| | | | | |
|---|---|---|---|---|
| | | 58 | A.T. unpublished | Nigeria, Zaria, Zaria |
| E. barbinodis Hack. | | 40 | Pienaar (1955) | South Africa, Pretoria Dist. |
| | | 40 | de Wet (1958) | South Africa, Transvaal |
| E. barrelieri Daveau | | 60 | Moffett and Hurcombe (1949) | Dominican Republic, Santiago |
| | 30 | | Gould (1960) | U.S.A., Texas, Mills Co. |
| | 30 | | Gould (1960) | U.S.A., Texas, Travis Co. |
| | 30 | | Gould (1960) | U.S.A., Texas, Lubbock Co. |
| | | 60 | Singh and Godward (1960) | France, Bot. Gard. Lyon |
| | 30 | | Gould and Soderstrom (1967) | Dominican Republic, Santiago |
| | | 60 | Jones, Ponti, Tavassoli and Dixon (1978) | Macronesia, Tenerife, Puerto de la Cruz |
| E. barteri C.E. Hubbard | 10 | | Dujardin (1978) | Zaire, Kinshasa, Lemba |
| E. beyrichii J.G. Smith | See E. secondiflora Presl. | | | |
| E. bicolor Nees | 10 | | Streetman (1963b) | U.S.D.A., Introduction |
| | | 20 | Jones, Ponti, Tavassoli and Dixon (1978) | Ethiopia, Shoa (Shewa), Debra Zeit |

| | | | | |
|---|---|---|---|---|
| E. bifaria (Vahl.) Wight | | 40 | Janaki Ammal (1945) | ? |
| E. biflora Hack. ex Schinz | | 20 | Moffett and Hurcombe (1949) | South Africa, Cape Prov., Mafeking |
| | | 20 | Moffett and Hurcombe (1949) | South Africa, Cape Prov., Kimberely |
| E. boriana Launert | | 60 | Murin and Sheikh (1971) | Iraq, Jadriya |
| E. botryodes W.D. Clayton | | 80 | A.T. unpublished | Ethiopia, Sidamo Borama, Between Yavello and Aghera Mariam |
| E. brownii (Kunth) Nees | | 40 | Janaki Ammal (1945) | ? |
| E. bulbillifera Steud. | | 40 | Tateoka (1954a) | Japan |
| | | 40 | Tateoka (1955) | Japan, Sirahama |
| E. burmanica Bor. | | 40 | Larsen (1963) | Thailand, Payap, Doi Sutep |
| | | 40 | Larsen (1963) | Thailand, Payap, Bo Luang Plateau |
| E. cambessediana (Kunth) Steud. | See E. gangetica (Roxb.) Steud. | | | |
| E. capensis (Thunb.) Trin. | | 40 | Avdulov (1928) | ? |
| | | 60 | Moffett and Hurcombe (1949) | Zimbabwe |

| | | | | |
|---|---|---|---|---|
| | | 40 | Pienaar (1955) | South Africa, Transvaal, Fochville |
| | | 40 | Pienaar (1955) | South Africa, Transvaal, Swartkop |
| | | 20 | de Wet (1958) | South Africa, Transvaal |
| | | 40 | A.T. unpublished | Zambia, Central Prov., Lusaka |
| E. capillaris (L.) Nees | 50 | | Gould (1958) | U.S.A., Texas, Brazos CO. |
| E. chalcantha Trin. | See E. racemosa (Thunb.) | | | |
| E. chapelieri (Kunth) Nees | | 20 | Moffett and Hurcombe (1949) | South Africa |
| | | 20 | Tateoka (1965a) | Madagascar, Tamatave |
| | | 20 | Auquier and Renard (1975) | Burundi, Bururi, Kigwena |
| | 10 | | Dujardin (1979b) | Zaire, Kinshasa, Mont Ngafula, Kimuenza |
| | | 20 | Dujardin (1979b) | Zaire, Kinshasa, Lemba |
| | | 20 | A.T. unpublished | Mozambique, Maputo, Manhica |
| | | 20 | A.T. unpublished | Zambia, Central Prov. Lusaka, Leopards` Hill |
| E. chariis (Schult) Hitch. | See E. nutans Retz. for count made by Mehra et al. (1968) (see Clayton (1974) explanation of nomenclature of E. chariis) and E. gangetica for count made by Janaki Amal (1945) (see Darlington and Wylie (1955) for alternative name) | | | |

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| E. chloromelas Steud. | | 40 | Pienaar (1955) | South Africa, Brankhorsts Pruit |
| | | 60 | Pienaar (1955) | South Africa, Transvaal, Johannesburg |
| | | 60 | Pienaar (1955) | South Africa, Transvaal, Fochville |
| | | 60 | Pienaar (1955) | South Africa, Transvaal, Swartkop |
| | | 61 | Pienaar (1955) | South Africa ,Transvaal, Johannesburg |
| | | 61 | Pienaar (1955) | South Africa, Transvaal, Swartkop |
| | | 61 | Pienaar (1955) | South Africa, Transvaal, Fochville |
| | | 62 | Pienaar (1955) | South Africa, Transvaal, Johannesburg |
| | | 62 | Pienaar (1955) | South Africa ,Transvaal, Pretoria |
| | | 62 | Pienaar (1955) | South Africa, Transvaal, Swartkop |
| | | 63 | Pienaar (1955) | South Africa, Transvaal, Johannesburg |
| | | 63 | Pienaar (1955) | South Africa, Transvaal, Pretoria |

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| | | 63 | Pienaar (1955) | South Africa, Transvaal, Swartkop |
| | 20 | | Streetman and Wright in Streetman (1963a) | U.S.D.A. Introduction |
| | 40 | | Streetman and Wright in Streetman (1963a) | U.S.D.A. Introduction |
| | 20 | | Vorster and Liebenberg (1977) | South Africa, Transvaal |
| | | ca 63 | A.T. unpublished | Portugal, Hortus botanicus Coimbra |
| E. cilianensis (All.) (Lut.) Syn.E. megastachya Link. | | 20 | Avdulov (1928) | ? |
| | | 20 | Parodi (1946) | Argentine, Buenos Aires |
| | 10 | | Heiser and Whitaker (1948) | U.S.A. |
| | | 20 | Moffett and Hurcombe (1949) | South Africa, Transvaal, Irene |
| | | 20 | Tateoka (1955) | Japan, Wakayama |
| | 10 | 20 | Singh and Godward (1960) | France, Lyon Botanical Garden |
| | 10 | | Gould (1960) | U.S.A., Texas, Mason Co. |

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| | 20 | Larsen (1963) | Thailand, Payap, Doi Sutep |
| | ca 40 | Larsen (1963) | Thailand, Payap, Doi Sutep |
| 35 | | Mehra, Khosla, Kohli and Koonar (1968) | India, Chandigarh |
| | 20 | Fernandes and Queirós (1969) | Portugal, Porto, Gondomar |
| | 20 | Fernandes and Queirós (1969) | Portugal, Coimbra, Souzelas |
| 10 | | Malik and Tripathi (1970) | India, Udaipur, Ragastan |
| 10 | | Reeder (1971) | Mexico, Chiuahua, 9 miles west of Jimenz |
| | 20 | Jones, Ponti, Tavassoli and Dixon (1978) | Portugal, Bira Litoral, Coimbra |
| | 40 | Jones, Ponti, Tavassoli and Dixon (1978) | Mozambique, Maputo, Deane-Namaacha |
| | 60 | Jones, Ponti, Tavassoli and Dixon (1978) | Ethiopia, Sidamo Borama, Negelli |

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| | 10 | | Dujardin (1979b) | Zaire, Bas-Zaire, Mbanza Ngungu, Mvuazi |
| | 10 | | Dujardin (1979b) | Zaire, Bandundu, Popokabaka, Lufuna |
| | | 20 | A.T. unpublished | France, Dordogne, Bergerac |
| E. ciliaris (L.) R.Br. | | 40 | Moffett and Hurcombe (1949) | South Africa |
| | | 20 | de Wet (1960) | South Africa |
| | | 20 | Tateoka (1962) | Mexico, Chipas, Tuxtla - Gutierrez |
| | | 20 | Tateoka (1965a) | Madagascar, Tamatava |
| | | 20 | Tateoka (1965b) | Tanzania, Morogoro |
| | 10 | | Mehra, Khosla, Kohli and Koonar (1968) | India, Chandigarh |
| | 10 | | Gould and Soderstrom (1970a) | Mexico, Yucatan |
| | | 20 | Dujardin (1978) | Zaire, Kinshasa, Lemba |
| | 10 | | Rao and Mwasumbi (1981) | Tanzania, Negerengeri |

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|---|---|---|---|---|
| | | 20 | A.T. unpublished | Mozambique, Maputo, Matola |
| | | 20 | A.T. unpublished | Uganda, Eastern Province, Serere |
| E. congesta Oliv. | | 40 | A.T. unpublished | Zimbabwe, Manicaland, Umtali, Uumba |
| E. curti-pedicillata Buckl. | | 40 | Brown (1951) | U.S.A., Texas |
| | 20 | | Gould (1968) | U.S.A., Texas, Mason Co. |
| | 20 | | Gould (1968) | U.S.A., Texas, Brazos Co. |
| E. curvula (Schrad.) Nees | | 40 | Neilsen (1939) | South Africa, Cape Prov., Kimberley |
| | | 50 | de Wet (1954) | South Africa, Pretoria, Horticultural Experimental Farm |
| | | 20 | Pienaar (1955) | South Africa, Cape Prov., Kimberley |
| | | 40 | Pienaar (1955) | South Africa, Transvaal, Ermelo |
| | | 40 | Pienaar (1955) | South Africa, Transvaal, Johannesburg (5 localities) |
| | | 40 | Pienaar (1955) | Tanzania |
| | | 60 | Pienaar (1955) | South Africa, Transvaal, Ermelo |

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| | 60 | Pienaar (1955) | South Africa, Transvaal, Schagen | |
| | 42 | de Winter (1955) | ? | |
| | 63 | de Winter (1955) | ? | |
| | 80 | de Winter (1955) | ? | |
| | 40 | de Wet (1958) | South Africa, Transvaal, | |
| 20 | | Streetman and Wright in Streetman (1963a) | U.S.D.A. Introduction | |
| 20 | | Mehra, Khosla, Kohli and Koonar (1968) | India, Chandigarh | |
| | 20 | Hutchinson in Voigt (1971) | U.S.D.A. Introduction, | |
| 10 | | Stalker and Wright (1975) | U.S.D.A. Introduction | |
| 20 | | Stalker and Wright (1975) | U.S.D.A. Introduction | |
| 20 | | Voster and Liebenberg (1977) | South Africa, Transvaal | |
| 25 | | Voster and Liebenberg (1977) | South Africa, Transvaal | |
| 30 | | Voster and Liebenberg (1977) | South Africa, Transvaal | (17 collections) |

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| | 40 | | Voster and Liebenberg (1977) | South Africa, Transvaal |
| | | 40 | A.T. unpublished | Germany, Botanischer Garten, Berlin - Dahlem |
| | | 40 | A.T. unpublished | Germany, Botanischer Garten, Munchen |
| | | 70 | A.T. unpublished | Ethiopia, Shoa, Debra Zeit |
| E. denudata Hack. | See E. nindensis Ficalho and Hiern | | | |
| E. diarrhena (Schult.) Steud. | 10 | | Roy (1965) | India, National Botanical Garden Lucknow |
| E. diffusa Buckl. | 30 | | Gould (1965) | Mexico, Toluca |
| | 30 | | Reeder (1968) | Mexico, Durango, Bermejillo |
| | 30 | | Reeder (1971) | Mexico, Chihuahua, Jimenez |
| | 30 | | Reeder (1971) | Mexico, Chihuahua, Jimenez |
| | 30 | | Reeder (1971) | Mexico, Chihuahua, Cuauhtemoc |
| | 30 | | Reeder (1971) | Mexico, Zacatacas, Villanueva |
| E. diplachnoides Steud. | See E. namaquensis Schrad. | | | |

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|---|---|---|---|---|
| E. domingensis (Pers.) Steud. | 20 | | Gould and Soderstrom (1970a) | Mexico, Yucatan |
| E. echinochloidea Stapf | | 40 | Moffett and Hurcombe (1949) | South Africa, Cape Prov., Barkley West |
| | | 40 | Pienaar (1955) | South Africa, Cape Prov., Kimberley |
| | | 30 | de Wet (1960) | South Africa |
| E. elongata (Willd) Jacqu. | | 40 | Avdulov (1931) | ? |
| E. ferruginea (Thunb.) Beauv. | | 80 | Tateoka (1953) | Japan |
| | | 80 | Tateoka (1954a) | Japan, Suginami |
| | | 80 | Tateoka (1967) | Japan, Kanyake, Itanogun, Tohushima Pref. |
| | | 80 | Tateoka (1967) | Japan, Motohashi, Gunma Pref. |
| | | 80 | Tateoka (1967) | Japan, Kobotoke -Ioge |
| E. frankii (C.A. Meyer) Steud. | 20 | | Koch (1974) | U.S.A., Missouri, Montgomery Co. |
| | 20 | | Koch (1974) | U.S.A., Illinois, Lake Co. |
| | 20 | | Koch (1974) | U.S.A., Illinois, Logan Co. |

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| | 20 | | Koch (1974) | U.S.A., Michigan, Monro Co. |
| | 20 | | Koch (1974) | U.S.A., Michigan, Monro Co. |
| | 20 | | Koch (1974) | U.S.A., Michigan, Monro Co. |
| | 40 | | Koch (1974) | U.S.A., Missouri, Montgomery Co. |
| E. galpinii Stent | See E. inamoena K. Schum. | | | |
| E. gangetica (Roxb.) Steud. Syn. E. cambessediana (Kunth) Steud. | 10 | | Hagerup (1932) | Africa, Mali, Timbouctou |
| | | 40 | Janaki Ammal (1945) | ? |
| | | 80 | Tateoka (1965b) | Kenya, Coast Province, Kwale |
| | 10 | | Dujardin (1979b) | Zaire, Kinshasa, Ngaliema, Island of Mimosas |
| | 10 | | Dujardin (1979b) | Zaire, Kinshasa, Matete |
| | | 20 | A.T. unpublished | Sierra - Leone, Northern Province, Freetown |
| | | 20 | A.T. unpublished | Nigeria, Zaria, Zaria |

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|---|---|---|---|---|
| E. glomerata (Walt.) L.H. Dewey | 10 | | Gould and Soderstrom (1967) | Brazil, Minas Gerais |
| | 10 | | Pohl and Davidse (1971) | Costa Rica, Alajuela, 2km. E. of Guacima |
| E. glutinosa (Swartz) Trin. | 30 | | Reeder (1968) | Mexico, Jalisco, Guadalajara |
| E. grandis Hillber. | | 44 | Skottsberg (1953) | Hawaii, Oahu |
| E. guianensis Hitchc. | 10 | | Davidse and Pohl (1974) | Venezuela, Amazonas, Puerto - Ayacucho |
| E. gummiflua Nees | | 40 | de Wet (1954) | South Africa, Pretoria, Horticultural Experimental Farm |
| | | 40 | Pienaar (1955) | South Africa, Transvaal, Fochville |
| E. habrantha Rendle | | 60 | Moffett and Hurcombe (1949) | Zimbabwe |
| | | 90 | Moffett and Hurcombe (1949) | Zimbabwe |
| E. heteromera Stapf Syn.E. wilmisii Stapf | | 40 | de Wet (1954) | South Africa, Pretoria, Horticultural Experimental Farm |
| | | 40 | de Wet (1958) | South Africa, Transvaal |
| | | 40 | de Wet (1960) | South Africa |

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| | | 41 | Jones, Ponti, Tavassoli and Dixon (1978) | Mozambique, Maputo, Namaacha |
| E. hierniana Rendle Syn. E. uniglumis Hack. | | 40 | Pienaar (1955) | South Africa, Distr. Pretoria |
| | | 40 | de Wet (1958) | South Africa, Transvaal |
| E. hirsuta (Michx.) Nees | 50 | | Gould (1958) | U.S.A., Texas, Robertson Co. |
| E. hondurensis Pohl | ca 20 | | Gould and Soderstrom (1970a) | Mexico, Oaxaca |
| | 20 | | Pohl (1980) | Honduras, 10.5 Km. S.E. of Yucaran |
| E. hypnoides (Lam.) B.S.P. | 10 | | Davidse and Pohl (1972) | Honduras, Morozan, El Zamorono |
| | 20 | | Davidse (1981) | U.S.A., Missouri, St. Charles Co. |
| | | 20 | Løve and Løve (1981) | Canada, Manitoba, King's Park |
| E. inamoena K. Schum. Syn. E. galpinii Stent | | 40 | Pienaar (1955) | South Africa, Distr. Pretoria |
| | | 41 | Pienaar (1955) | South Africa, Frankenwald Experimental Station |
| E. intermedia Hitchc. Syn. E. lugens Nees | 20 | | Gould (1958) | U.S.A., Texas, Brook Co. |

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|---|---|---|---|---|
| (two collections) | 40 | | Gould (1958) | U.S.A., Texas, Brazos Co. |
| | ca 54 | | Gould (1958) | U.S.A., Texas, Uvalde Co. |
| | 20 | | Streetman (1963b) | U.S.A. |
| cf. intermedia | 38 | | Reeder (1968) | Mexico, Tamascaltepec |
| | 36 | | Gould (1968a) | U.S.A., Texas, Falls Co. |
| | 36 | | Gould (1968a) | U.S.A., Texas, Kenedy Co. |
| | 40 | | Gould (1968a) | U.S.A., Texas, Lelano Co. |
| | 50 | | Gould (1968a) | U.S.A., Texas, Kerr Co. |
| | ca 54 | | Gould (1968a) | U.S.A., Texas, Edwards Co. |
| | 60 | | Gould (1968a) | U.S.A., Texas, Maverick Co. |
| | 30 | | Reeder (1971) | Mexico, Nuevo Leon, Galeana |
| | ca 37 | | Reeder (1971) | Mexico, Durango, Llano Grande |
| | 40 | | Reeder (1971) | Mexico, Durango, Rio Chico |
| | ca 60 | | Reeder (1971) | Mexico, Guanajuato, Dolores Hidalgo |

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| | ca 60 | | Reeder (1971) | Mexico, Chihuahua, Villa Matomoros |
| E. japonica (Thunb.) Trin. | | 20 | Avdulov (1928) | ? |
| | | 20 | Larsen (1963) | Thailand, Payap, Chiengmai |
| | 20 | | Gould and Soderstrom (1974) | Ceylon, Eastern Province |
| | | 60 | Christopher and Abraham (1974) | South India, Kallikkand |
| | 10 | | Mehra and Kalia (1976) | India, Assam, Gauhati |
| | 10 | | Kalia (1978) | North East of India |
| E. kiwuensis Jedw. | | 40 | A.T. unpublished | Ethiopia, Sidamo Borama, between Yirga Alem to Negelli |
| E. lappula Nees | | 40 | de wet (1954) | South Africa, Pretoria, Horticultural Experimental Farm |
| | | 40 | de Wet and Anderson (1956) | South Africa, Transvaal, |
| | | 40 | de Wet (1958) | South Africa, Transvaal |
| E. lasiantha Stapf | See E. olivacea K. Schum. | | | |
| E. lehmanniana Nees | | 40 | Pienaar (1955) | South Africa, Prinshof Experimental Station |

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| | 30 | | Gould (1960) | U.S.A., Texas, Brazos Co. |
| | 20 | | Streetman and Wright in Streetman (1963a) | U.S.D.A. Introduction |
| | 25 | | Streetman and Wright in Streetman (1963a) | U.S.D.A. Introduction |
| | | 40 | Gould (1964) | U.S.A., Texas, Hudspeth Co. |
| | | 40 | A.T. unpublished | U.S.A., Department of Agriculture, Texas Plant Material Centre |
| E. linearis (Schum. and Thon.) Benth | 40 | | Hagerup (1932) | Africa, Mali, Timbouctou |
| E. macilenta (A. Rich.) Steud. | | 40 | Tateoka (1965b) | Kenya, Nairobi |
| | | 40 | Tateoka (1965b) | Uganda, Kampala |
| E. maderaspanta Bor | 30 | | Sharma, Berhe and Dash (1976) | India, Coastal Orissa |
| E. magaritacea Stapf | See E. rotifer Rendle | | | |
| E. maypurensis (H.B.K.) Steud | 20 | | Gould and Soderstrom (1967) | Surinam, Suriname, Zuid River |
| | 10 | | Gould and Soderstrom (1970a) | Mexico, Chiapas |

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| | 10 | | Pohl and Davidse (1971) | Costa Rica, Guanacaste, Bagaces |
| | 10 | | Davidse and Pohl (1974) | Venezuela, Amazonas, Puerto Ayacucho |
| | 10 | | Davidse and Pohl (1974) | Venezuela, Guarico, 12 Km.South of Calabozo |
| E. megalosperma F. Muell. ex Benth | | 20 | Singh and Godward (1960) | Australia, Queenland |
| E. megastachya (Koel.) Link. | See E. cilianensis (All.) Lut. | | | |
| E. mexicana (Hornem.) Link. Syn. E. neomexicana Vasey | | 60 | Avdulov (1928) | ? |
| | | 60 | Parodi (1946) | Argentine (Introduced) |
| | 28 | 56 | Singh and Godward (1960) | Sweden, Uppsala University Botanic Garden |
| | 30 | | Gould (1966) | Mexico, Oaxaca, Oaxaca |
| | 30 | | Reeder (1968) | Mexico, Temascaltepec |
| | 30 | | Reeder (1971) | Mexico, Chihuahua, Cuauktemo |
| | 30 | | Pohl and Davidse (1971) | Costa Rica, Alajuela, Palmeres |

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| | | 60 | Pohl and Davidse (1971) | Costa Rica, San Jose, Ciudad University |
| | | ca 60 | Kerguelen (1975) | France, Gironde, near Bordeaux |
| | 30 | | Davidse and Pohl (1978) | Costa Rica, Alajuela, 3km. S. of the Palmares exit |
| | | 60 | Jones , Ponti, Tavassoli and Dixon (1978) | Germany, Botanischer Garten, Berlin - Dahlem |
| | | 60 | Jones, Ponti, Tavassoli and Dixon (1978) | Norway, Oslo, Hortus Botanicus Universitatis |
| E. micrantha Hack. | | 40 | Pienaar (1955) | South Africa, Transvaal, Swartkop |
| | | 41 | Pienaar (1955) | South Africa, Transvaal, Swartkop |
| | | 40 | de Wet (1958) | South Africa, Transvaal |
| E. mildbraedii Pilger | | 20 | Tateoka (1965b) | Uganda, Kampala |
| E. minor Host Syn. E. poaeoides P. Beauv. | | 40 | Sokolovskaya and Strelkova (1939) | ? |
| | | 40 | Ono and Tateoka (1953) | Japan, Simosuwa |

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| | 40 | Tateoka (1954b) | Japan | |
| | 30 | Mulay and Jardisan (1956) | India, Rajastan Desert | |
| 20 | | Swami (1963) | India, Andhra Pradesh | |
| 20 | | Mehra, Khosla, Kohli and Koonar (1968) | India, Chandigarh | |
| | 40 | Fernandes and Quiros (1969) | Portugal, Porto, Vila Nova de Gaia | |
| | 40 | Murin in Majovsky et al. (1974) | Slovakya, Podunajká nižina, Bratislava - Nové Mesto | |
| 30 | | Reeder (1977) | U.S.A., Texas, Culberson Co. | |
| | 40 | Petrova in Prokudin, Vovk, Petrova, Ermolenko and Verichenko (1977) | ? | |
| | 40 | Sokolovskaya and Probatova (1978) | U.S.S.R., Dagastan Republic, Kumto-Kala | |
| | 40 | Sokolovskaya and Probatova (1978) | U.S.S.R., Dagastan Republic, Kharakhi | |

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| | 40 | Sokolovskaya and Probatova (1978) | U.S.S.R., Armenian Republic, near Pilizham |
| | 40 | Sokolovskaya and Probatova (1978) | U.S.S.R., Western Pamir, Khorog |
| | 40 | Jones, Ponti, Tavassoli and Dixon (1978) | France, Gard, Nimes |
| | 40 | Jones, Ponti, Tavassoli and Dixon (1978) | U.S.S.R., Botanical Garden of Armenian Academy of Sciences, Tashkent |
| | 20 | Guzik and Levkovsky (1979) | U.S.S.R. |
| 22 | | Parfit and Harriman (1981) | U.S.A., Wisconsin, Winnebago Co. |
| | 20 | A.T. unpublished | Germany, Botanischer Garten, Berlin - Dahlem |
| 20 | | A.T. unpublished | U.S.S.R., Botanical Garden of Uzbek Academy of Sciences, Erevan |
| | 40 | A.T. unpublished | France, Dordogne, Bergerac |

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| | | 40 | A.T. unpublished | France, Lot, Castelfranc |
| E. montufaria (H.B.K.) Steud. | | 70 | Bowden and Senn (1962) | Bolivia, Cochobamba |
| E. multicaulis Steud. | | 40 | Ono and Tateoka (1953) | Japan, Suginami |
| | | 40 | Tateoka (1954b) | Japan |
| | | 40 | Tateoka (1967) | Japan, Kanyake, Itanogun, Tokushima Pref. |
| | | 40 | Tateoka (1967) | Japan, Kobotoketoge, Tokyo |
| E. multispicula Kitagawa | | 40 | Ono and Tateoka (1953) | Japan, Koremasa |
| E. namaquensis Schard. var. namaquensis | | 20 | Moffett and Hurcombe (1949) | South Africa |
| | | 20 | Tateoka (1965b) | Tanzania, Morogoro |
| | 10 | | Dujardin (1979b) | Zaire, Bas-Zaire, Kazangulu, Sabuka |
| var. diplachnoides (Steud.) W.D. Clayton | 20 | | Mehra, Khosla, Kohli and Koonar (1968) | India, Chandigarh |
| | | 20 | Christopher and Abraham (1974) | South India, Mahendragiri |

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| | 10 | | Gould and Soderstrom (1974) | Ceylon, North - Central Province |
| | 10 | | Gould and Soderstrom (1974) | Ceylon, Central Province |
| | | 20 | A.T. unpublished | Nigeria, Zaria, Zaria |
| | | 20 | A.T. unpublished | Ghana, Northern Region, Mole Game Reserve |
| E. neomexicana Vasey | See E. mexicana (Hornem.) Link | | | |
| E. nigra Steud. | 20 | | Mehra, Khosla, Kohli and Koonar (1968) | India, Kalka |
| | 30 | | Christopher (1976) | India, Kerala, Trivandrum |
| | 30 | | Kalia (1978) | North - Eastern India |
| E. nindensis Ficalho and Hiern. Syn. E. denudata Hack. | | 40 | Moffett and Hurcombe (1949) | South Africa |
| | | 20 | de Wet and Anderson (1956) | South Africa, Transvaal |
| | | 20 | de Wet (1960) | South Africa |
| E. nutans (Retz.) Steud. Syn. E. chariis (Schult.) Hitchc. | 30 | | Chen and Hsu (1962) | Taiwan |

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| | 20 | | Mehra, Khosla, Kohli and Koonar (1968) | India, Chandigarh |
| | 30 | | Gould and Soderstrom (1974) | Ceylon, Northern Province |
| | 30 | | Gould and Soderstrom (1974) | Ceylon, Eastern Province |
| | 30 | | Christopher and Abraham (1974) | South India |
| | 21 +f | | Kalia (1978) | North Eastern India |
| E. obtusa Munro | | 40 | Moffett and Hurcombe (1949) | South Africa, Cape Province, Kimberley |
| | | 40 | Pienaar (1955) | South Africa, Cape Province, Kimberley |
| | | 20 | de Wet (1960) | South Africa |
| | 20 | | Streetman (1963b) | U.S.D.A. Introduction |
| | 10 | | Busey (1976) | South Africa, Orange Free State, Glen Agricultural College |
| E. obtusiflora (Fourn.) Scribn. | 20 | | Reeder (1977) | U.S.A., Arizona, Cochise Co. |
| E. olivacea K. Schum. Syn. E. lasiantha Stapf | | 20 | Tateoka (1965b) | Tanzania, Mt. Kilimanjaro |

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| | | 20 | Tateoka (1965b) | Kenya, Eastern Midland, Thike |
| E. orcuttiana Vasey | | 20 | A.T. unpublished | France, Gironde, Hastignan, St. Medard en Jalle |
| E. oxylepis (Torr.) Torr. | See E. secundiflora Presl. | | | |
| E. pallens Hack. | | 20 | Moffett and Hurcombe (1945) | South Africa, N. Cape, Andalusia |
| E. pallescens Hitchc. | See E. linearis made by Hagerup (1932) (see Darlington and Wylie (1955) for alternative name) | | | |
| E. palmeri S. Watson | 20 | | Reeder (1971) | Mexico, Durango, La Zarca |
| E. paniciformis (A. Br.) Steud. | | 60 | Tateoka (1965b) | Kenya, Nakuru |
| E. papposa (Roem. and Schult.) | | 20 | Gould and Soderstrom (1970b) | Tunisia, Kassering |
| | | 20 | Gould and Soderstrom (1970b) | Tunisia, Djebel Bou Hodma |
| | | 40 | Jones, Ponti, Tavassoli and Dixon (1978) | Ethiopia, Harar, Degahabur (Deghabur) |
| E. patens Oliv. | | 20 | Moffett and Hurcombe (1949) | South Africa |
| | 10 | | Dujardin (1979a) | Zaire, Equateur, Mampono, bank of River Maringa |

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| | | 20 | Dujardin (1979b) | Zaire, Bas Zaire, Kasangulu, Zongo Falls |
| | | 20 | A.T. unpublished | Zimbabwe, Manicaland, Umtali, Uumba |
| E. pectinacea (Michx.) Nees | 20 | | Gould (1958) | U.S.A., Texas, Travis Co. |
| | 30 | | Gould (1958) | U.S.A., Texas, Palo Pinto Co. |
| | 30 | | Gould (1958) | Mexico, North of Chihuahua |
| | ca 30 | | Gould (1966) | Mexico, 20 miles S.E. of Mexico City |
| | 40 | | Gould (1966) | Mexico, Baja California, Sur la Paz |
| | 30 | | Koch (1974) | U.S.A., Arizona, Apache Co. |
| | 30 | | Koch (1974) | U.S.A., Arkansas, Independent Co. |
| | 30 | | Koch (1974) | U.S.A., California, Mandocino Co. |
| | 30 | | Koch (1974) | U.S.A., Florida, Dade Co. |
| | 30 | | Koch (1974) | U.S.A., Illinois, Logan Co. |
| | 30 | | Koch (1974) | U.S.A., Kansas, Barber Co. |

| | | | | | |
|---|---|---|---|---|---|
| | 30 | | Koch (1974) | U.S.A., Kansas, Comanche Co. |
| | 30 | | Koch (1974) | U.S.A., Kasas, Douglas Co. |
| | 30 | | Koch (1974) | U.S.A., Kansas, Morton Co. |
| | 30 | | Koch (1974) | U.S.A., Louisiana, Allen Parish Co. U.S.A., |
| | 30 | | Koch (1974) | Massachusetts, Suffolk Co. |
| | 30 | | Koch (1974) | U.S.A., Michigan, Monro Co. U.S.A., |
| | 30 | | Koch (1974) | Michigan, Washtenaw Co. |
| | 30 | | Koch (1974) | U.S.A., Missouri, St. Charles Co. |
| | 30 | | Koch (1974) | U.S.A., North Carolina, Durham Co. |
| | 30 | | Koch (1974) | Mexico, Aguascalientes |
| (3 collections) | 30 | | Koch (1974) | Mexico, Jalisco |
| | 30 | | Koch (1974) | Mexico |
| | | 60 | Kerguelen (1975) | France, Tarn et Garonne, Castelsarrasin |
| | 30 | | Davidse (1981) | U.S.A., Missouri, St. Charles Co. |

| | | | | |
|---|---|---|---|---|
| | | 60 | A.T. unpublished | France, Gironde, la Haillau |
| | | 60 | A.T. unpublished | Hungary, Hortus Botanicus Vacratot |
| E. pilosa (L.) P. Beauv. ●▲ | | 40 | Tateoka (1954b) | Japan |
| | | 60 | Bowden and Senn (1962) | Argentina, Jujuy Airport |
| | | 40 | Tateoka (1965b) | Kenya, Nairobi |
| | 20 | | Mehra, Khosla, Kohli and Koonar (1968) | India, Solan |
| | 10 | | Baquar and Manzoor Saeed (1969) | Pakistan, Karachi, Central Lab. Campus |
| | | 40 | Fernandes and Queirós (1969) | Portugal, Porto, Vila Nova de Gaia |
| | | 40 | Fernandes and Queirós (1969) | Portugal, Coimbra, Montemor - o - Velho |
| | 20 | | Christopher and Abraham (1974) | South India |
| | 20 | | Koch (1974) | U.S.A., Arkansas, Pulaski Co. |
| | 20 | | Koch (1974) | U.S.A., Florida, Collier Co. |

| | | | | |
|---|---|---|---|---|
| | 20 | | Koch (1974) | U.S.A., Florida, Dade Co. |
| (2 collections) | 20 | | Koch (1974) | U.S.A., Massachusetts, Hampshire Co. |
| | 20 | | Koch (1974) | U.S.A., North Carolina, Orange Co. |
| | 20 | | Koch (1974) | U.S.A., Texas, Jefferson Co. |
| | 20 | | Koch (1974) | Dominican Republic, Hispaniola |
| | 20 | | Koch (1974) | Jamaica |
| | 20 | | Koch (1974) | Mexico, Oaxaca |
| | 25 | 50 | Mukherjee (1978) | West Bengal, Chinsurah, Rice Research Staion |
| | | 40▲ | Sokolovskaya and Probatova (1978) | U.S.S.R., Western Pamir, Khorog |
| | 20 | 40 | Jones, Ponti, Tavassoli and Dixon (1978) | Portugal, Beira Litoral, Montemor - o - Velho |
| | | 40 | Jones, Ponti, Tavassoli and Dixon (1978) | U.S.S.R., Botanical Garden of Armenian Academy of Sciences, Erevan |
| | 20 | | Rao and Mwasumbi (1981) | Tanzania, Dar es Salaam University Campus |

| | | | | |
|---|---|---|---|---|
| E. plana Nees | | 20 | Pienaar (1955) | South Africa, Transvaal, Swartkop |
| | | 20 | Pienaar (1955) | South Africa, Transvaal, Johannesburg |
| | | 20 | Pienaar (1955) | South Africa, Transvaal, Devon |
| | 10 | | Streetman (1963b) | U.S.D.A. Introduction |
| | 10 | | Busey (1976) | South Africa, Natal, near Dargle |
| | | 20 | A.T. unpublished | Ethiopia, Shoa (Shewa), Debra Zeit |
| E. plumbea Scribn. | 30 | | Gould (1965) | Mexico, Michoacan, Hidalgo |
| | | 60 | Reeder (1984) | Mexico, Zacatecas, 8 Km. East of Monte Escobedo |
| E. polytricha Nees | ca 30 | | Gould and Sodesrom (1967) | Brazil, Goias |
| E. porosa Nees | | 40 | A.T. unpublished | Zimbabwe, Matabeleland, Matopos |
| E. prolifera (Swartz) Steud. | 20 | | Davidse and Pohl (1972) | Honduras, Choluteca, Cendeño |
| | 20 | | Davidse and Pohl (1972) | Nicaragua, Chinandega, Corinto |

| | | | | |
|---|---|---|---|---|
| | 10 | | Dujardin (1978) | Zaire, Bas Zaire, Boma, Moanda |
| E. pseudo-sclerantha Chiov. | | 50 | de Wet (1960) | South Africa |
| E. racemosa (Thunb.) Syn. E. chalcantha Trin. | | 60 | Pienaar (1955) | South Africa, Transvaal, Swartkop |
| | | 62 | Pienaar (1955) | South Africa, Transvaal, Swartkop |
| | | 60 | de Wet (1958) | South Africa, Transvaal |
| | | 40 | Tateoka (1965b) | Tanzania, Kilimanjaro, Kibo |
| | | 20 | A.T. unpublished | Uganda, Eastern Province, Serere |
| E. reptans[Δ] Nees | 30 | | Gould (1968a) | U.S.A., Texas |
| E. rigidior Pilg. | | 40 | de Wet (1960) | South Africa |
| | | 40 | A.T. unpublished | Zimbabwe, Matabeleland, Matopos |
| E. robusta Stent | | 70 | Pienaar (1955) | South Africa, Transvaal, Swartkop |
| (two strains) | | 70 | Pienaar (1955) | South Africa, Transvaal, Pretoria |
| | | 70 | Pienaar (1955) | South Africa, Transvaal, Johannesburg |

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|---|---|---|---|---|
| | | 70 | Pienaar (1955) | South Africa, Transvaal, Johannesburg |
| | | 70 | Pienaar (1955) | South Africa, Transvaal, Johannesburg |
| | | 80 | Pienaar (1955) | South Africa, Transvaal, Swartkop |
| E. rotifer Rendle | | 40 | Moffett and Hurcombe (1949) | South Africa |
| | | 40 | Nordenstam (1969) | Namibia, Omaruru, Distr. Brandberg |
| E. schweinfurthii Chiov. | | 40 | A.T. unpublished | Ethiopia, Sidamo Borama, Kebra Mengist near Wadera |
| E. scaligera Salzm. ex Steud. | 20 | | Koch (1978) | U.S.A., Southern Florida |
| E. sclerantha Nees | | 40 | Moffett and Hurcombe (1949) | Zimbabwe |
| | | 40 | Moffett and Hurcombe (1949) | Zimbabwe |
| E. secundiflora Presl. Syn. E. oxylepis (Torr.) Torr. and E. beyrichii J.G. Smith | | 40 | Brown (1950) | U.S.A., Texas |
| | | 40 | Brown (1950) | U.S.A., Texas |
| | 20 | | Gould (1968a) | U.S.A., Texas, Comanche Co. |
| | 20 | | Gould (1968a) | U.S.A., Texas, Llano Co. |
| | 20 | | Gould (1968a) | U.S.A., Texas, Kleberg Co. |

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|---|---|---|---|---|
| E. sessilispica Buckl. | | 40 | Nielsen (1939) | U.S.A., Oklahoma Caddo Co. |
| | 20 | | de Lisle (1965) | U.S.A., Texas, Brooks Co. |
| | 20 | | Gould (1968a) | U.S.A., Texas Falls Co. |
| E. simpliciflora (Presl.) Steud. | 20 | | Pohl and Davidse (1971) | Costa Rica, Alajuela, 3 Km. South of San Pedro de Poas |
| E. spectabilis (Pursh.) Steud. | | 40 | Nielsen (1939) | Unknown |
| | | 20 | Sherif, Smith and Hornberger (1983) | U.S.A., Arkansas, near Fayetteville Airport |
| E. spicata Vasey | | 40 | Brown (1950) | U.S.A., Texas |
| E. sporoboloides Stapf | | 60 | Pienaar (1955) | South Africa, Transvaal, Frankenwald Experimental Station |
| E. squamata (Lam.) Steud. | 20 | | Dujardin (1978) | Zaire, Bas-Zaire, Kasangulu, Mfuti |
| | | 40 | A.T. unpublished | Sierra - Leone, Northern Province, Freetown |
| E. staphii de Winter | | 20 | de Wet (1960) | South Africa |
| E. suaveolens Koch | | 30 | Guzik and Lovkovsky (1979) | U.S.S.R. |

| | | | | |
|---|---|---|---|---|
| E. superba Peyr. | | 40 | Moffett and Hurcombe (1949) | South Africa, Cape Province, Kimberley |
| | | 40 | de wet (1954) | South Africa, Pretoria, Horticultural Experimental Farm |
| | | 40 | Pienaar (1955) | South Africa, Irene |
| | 20 | | Streetman and Wright in Streetman (1963a) | U.S.D.A. Introduction |
| | 20 | | Mehra, Khosla, Kohli and Koonar (1968) | India, Solan |
| | | 40 | Shanthamma, Narayan and Shukur (1976) | India, Mysore State, Manasagangotri |
| | 20 | | Reeder (1977) | U.S.A., Arizona, Santa Cruz Co. |
| | | 20 | Dujardin (1978) | Zaire, Kinshsa, Matete |
| | 20 | | Rao and Mwasumbi (1981) | Tanzania, Dar-es- Salaam Univesity Campus |
| | | 40 | A.T. unpublished | Uganda, Eastern Province, Serere |
| | | 40 | A.T. unpublished | Ghana, Eastern Province, Accra , Nurgua |

| | | | | |
|---|---|---|---|---|
| | | 40 | A.T. unpublished | Mozambique, Maputo, Namaacha |
| E. swallenii Hitchc. | 42 | | Gould (1968a) | U.S.A., Texas, Kleberg Co. |
| E. tef (Zucc.) Trotter Syn. E. abyssinica Link | | 40 | Avdulov (1928) | ? |
| | | 40 | Avdulov (1931) | ? |
| | | 40 | Parodi (1946) | Argentine cultivated |
| | | 40 | Moffett and Hurcombe (1949) | Zimbabwe |
| | | 40 | Mulugeta Assefa (1972) | Ethiopia |
| (6 accessions) | | 40 | Jones, Ponti, Tavassoli and Dixon (1978) | Ethiopia, Shoa (Shewa), Debra Zeit |
| | | 40 | A.T. unpublished | " " |
| E. tenella (L.) Roem. and Schult. | 10 | | Chen and Hsu (1962) | Taiwan |
| | 10 | | Swami (1963) | India, Andhra Pradesh |
| | | 20 | Larsen (1963) | Thailand, Payap, Doi Sutep |
| | | 20 | Larsen (1963) | Thailand, Payap, Chiengmai |

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|---|---|---|---|---|
| | | 20 | Larsen (1963) | Thailand, Pistsanulok, Sukhothai |
| | | 20 | Tateoka (1965a) | Japan |
| | 10 | | Mehra, Khosla, Kohli and Koonar (1968) | India, Chandigarh |
| | 10 | | Baquer and Manzoor Saeed (1969) | Pakistan, Karachi University Campus |
| | 30 | | Christopher and Abraham (1974) | South India |
| var. tenella | 10 | | Gould and Soderstrom (1974) | Ceylon, Northern Province |
| var. tenella | 30 | | Gould and Soderstrom (1974) | Ceylon, Central Province |
| var. insularis C.E.Hubb. | 20 | | Gould and Soderstrom (1974) | Ceylon, Central Province |
| var. insularis C.E.Hubb. | 30 | | Gould and Soderstrom (1974) | Ceylon, Eastern Province |
| | 10 | | Olorode (1975) | Nigeria, University Campus Ile Ife |
| | 10 | | Dujardin (1979b) | Zaire, Kinshasa, Lemba |
| | | 20 | A.T. unpublished | Sierra Leone, Northern Province, Freetown |

| | | | | |
|---|---|---|---|---|
| E. tenuifolia (A. Rich.) Steud. | | 40 | Tateoka (1965b) | Kenya, Nairobi |
| | | 40 | Tateoka (1965b) | Uganda, Mengo, Port Bell |
| | | 40 | Tateoka (1965b) | Tanzania, Morogoro |
| | 20 | | Pohl and Davidse (1971) | Costa Rica, San Jose, San Blas de Moravia |
| | 20 | | Gould and Soderstrom (1974) | Ceylon, Central Province |
| | 20 | | Dujardin (1979a) | Zaire, Equateur, Mompono bank of River Maringa |
| | 20 | | Dujardin (1979b) | Zaire, Bas - Zaire, Madimba, Ngidinga, 60 Km. South East of Kisantu |
| | | 40 | A.T. unpublished | Ethiopia, Shoa (Shewa), East of Lake Zwai |
| | | 40 | A.T. unpublished | Ethiopia, Sidamo Borama, between Yirga Alem and Negelli |
| | | 40 | A.T. unpublished | Ethiopia, Sidamo Borama, Lake Awasa |
| | | 40 | A.T. unpublished | Zambia, Northern Province, Makulu Mont. |

| | | | | |
|---|---|---|---|---|
| | | 41 | A.T. unpublished | Ethiopia, Sidamo Borama, between Yavello and Aghera Mariam |
| E. tephrosantos Schult. | 30 | | Koch (1974) | Mexico, Jalisco |
| | 30 | | Koch (1974) | Mexico, Mexico |
| | 30 | | Koch (1974) | Mexico, Morelos |
| | 30 | | Koch (1974) | Costa Rica, |
| | 30 | | Koch (1974) | Panama |
| | 30 | | Koch (1974) | U.S.A., Texas, Deaf Smith Co. |
| E. thollonii Frank | 10 | | Dujardin (1978) | Zaire, Kinshasa, Mont Ngufula , Funa Valley |
| E. tracyi Hitchc. | 30 | | Koch (1974) | U.S.A., St. Petersburg Beach, Pinellas Co. |
| | 30 | | Koch (1974) | U.S.A., Venice, Sarasota Co. |
| (3 accessions) | 30 | | Koch (1974) | U.S.A., Sanibel Island, Lee Co. |
| | 30 | | Koch (1974) | U.S.A., Longboat Key, Sarasota Co. |
| E. tremula Steud. | | 20 | Mulay and Leelamma (1956) | India, Rajputana Desert |
| | | 30 | Mulay and Prasad (1956) | India, Rajastan |

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|---|---|---|---|---|
| | | 20 | Tateoka (1965b) | Uganda, Bunyoro, Masindi |
| | 20 | | Christopher and Abraham (1974) | South India, Aryankavu |
| | 10 | | Dujardin (1979) | Zaire, Kinshasa, Lemba |
| E. trichocolea Hack. and Arech. | 40 | | Gould and Soderstrom (1970a) | Mexico, Chiapas |
| | 30 | | Davidse and Pohl (1972) | Honduras, El Paraiso, 23 Km. west of Danli |
| E. trichodes (Nutt.) Wood | | 40 | Mehra, Khosla, Kohli and Koonar (1968) | India, Solan |
| | 20 | | Reeder (1977) | U.S.A., Nebraska, Grant Co. |
| | | 40 | A.T. unpublished | U.S.A., Department of Agriculture, Texas Plant Material Centre |
| | | 40 | A.T. unpublished | U.S.A., Department of Agriculture, Kansas plant Material Centre |
| | | 40 | A.T. unpublished | U.S.A., Department of Agriculture, Nebraska, Miller collection |

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|---|---|---|---|---|
| E. truncata Hack. | | 20 | Moffett and Hurcombe (1949) | South Africa, Orange Free State, Fauresmith |
| E. uniglumis Hack. | See E. hiernina Rendle | | | |
| E. unioloides (Retz.) Nees ex Steud. | | 20 | Larsen (1963) | Thailand, Payap, Doi Sutep |
| | | ca 30 | Larsen (1963) | Thailand, Payap, Doi Sutep |
| | 20 | | Mehra, Khosla, Kohli and Koonar (1968) | India, Solan |
| | 9 | | Mehra and Sharma (1973) | Himalaya, Kathgodam, Nainital |
| | 10 | | Gould and Soderstrom (1974) | Ceylon, Central Province |
| | 10 | | Christopher and Abraham (1974) | South India, Malampuzha |
| | 10 | | Dujardin and Breyne (1975) | Cameroons, Douala |
| | 10 | | Kalia (1978) | North - Eastern India |
| | | 20 | A.T. unpublished | Sierra Leone, Northern Province, Freetown |
| E. usambarensis Napper (two collections) | | 80 | Tateoka (1965b) | Tanzania, Mt. Kilimanjaro |

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|---|---|---|---|---|
| E. variabilis (Guad.) Hbd. | 20 | | Carr (1978) | Oahu, Diamond Head |
| | 20 | | Carr (1978) | Oahu, Waianac Mts., Makaleha |
| E. viscosa (Retz.) Trin. | | 40 | Moffett and Hurcombe (1949) | Zimbabwe |
| | | 40 | de Wet (1958) | South Africa, Transvaal |
| | | 60 | Tateoka (1962) | Mexico, Chiapas, Tuxtla - Gutierrez |
| | 20 | | Gould and Soderstrom (1970a) see also E. hondurensis | Mexico, Chiapas |
| | 30 | | Gould and Soderstrom (1970a) | Mexico, Chiapas |
| | 30 | | Davidse and Pohl (1974) | Venezuela, Guarico, Estacion Biologica de Los Llanos |
| | | 60 | Reeder (1984) | Mexico, Baja California Sur, Todos Santos Jct. |
| E. wilmaniae C.E.Hubb. et Schweick. | | 20 | Moffett and Hurcombe (1949) | South Africa, Hay Division, Griqualand West |
| E. wilmsii Stapf | See E. heteromera Stapf | | | |

| | | | | |
|---|---|---|---|---|
| E. zeylanica Nees | | 36 | Larsen (1963) | Thailand, Payap, Doi Sutep |
| | | 40 | Larsen (1963) | Thailand, Payap, Doi Sutep |
| | | 40 | Larsen (1963) | Thailand, Surat, Ranawng |
| | | 60 | Larsen (1963) | Thailand, Ayuthia, Saraburi |
| | | ca 40 | Larsen (1963) | Thailand, Prachinburi, Cholburi |
| | | ca 80 | Larsen (1963) | Thailand, Prachinburi, Cholburi |
| ⧄ E. camerounensis W.D.Clayton | | 40 | J.K.Morton unpublished | Cameroons, Bamenda |
| ⧄ E. decanensis Bor. | | 20 | Christopher and Samaraj (1985) | India, The Nilgiris, Hosur |

Notes:

○ This species is now treated as Eragrostiella bifaria (Vahl.) Bor. by Philips, 1974.

□ The count for E. megastachya syn. of E. cilianensis published by Tateoka and Ono (1953) refers to E. poaeoides syn. of E. minor (Tateoka, 1955).

▽ The count for E. viscosa from Oaxaca by Gould and Soderstrom (1970a) refers to E. hondurensis (Pohl,1980)

● The count for E. pilosa published by Ono and Tateoka

(1953) refers to E. multispicula (Tateoka, 1965).

▲ The counts of 2n=35 for this species published by Sokolovskaya and Strelkova (1939) proved on subsequent examination to be 2n=40 (Sokolovskaya and Probatova, 1978).

△ This species is treated as Neeragrostis reptans (Michx.) Nicara (in Gould, 1968b).

■ The count of 2n=42 for this species, published by Nielsen and Humphrey (1937) proved on subsequent examination to be 2n=40 (Nielsen, 1939).

▼ These authors published a further count for this species in 1975, but the voucher number they cite indicates that this count was made on plants from the same collection as their earlier report in 1973.

⧄ These species came to my notice too late to be included in the text.

Appendix 2: Table 5 from Leigh (1980)

Chromosome counts of E. curvula strains

| | |
|---|---|
| Robusta blue | |
| E. robusta No.137 Grootfontein | ca.57<br>ca.52 |
| E. robusta No.98 Schagan | ca.62-65 |
| E. robusta No.13 Schagan | ca.53<br>ca.55 |
| Robusta intermediata | |
| E. curvula No.11 Valido | ca.40<br>or 41<br>ca.40<br>or 41 |
| Robusta green | |
| E. robusta No.99 Athol | ca.30<br>ca.30 |
| Curvula | |
| E. curvula No.12 Riotvlei | ca.40<br>or 41 |
| E. curvula No.9 Ermelo | ca.40 |
| E. curvula No.10 Tangangika | ca.40 |
| Chloromelas | |
| E. curvula No.81 | ca.59 |
| E. chloromelas No.79 | ca.60 |

(See pages19 and139for references to Leigh's work)

Appendix 3 Sources of the seeds of Eragrostis species studied by the present author

| Accession Number | Species | Source |
|---|---|---|
| 75-1 | E. aethiopica | United States Department of Agriculture ; Plant Inventory No. 364-801 |
| 75-144 | E. aspera | Royal Botanic Garden, Kew, Richmond, U.K. |
| 75-61 | E. atrovirens | Dr. P. Leeuw, Shika Research Station, (via Prof. B.J.Harris, Botany Department Ahmedo Bello University, Zaria ) Nigeria |
| 74-1 | E. barrelieri | Dr. B.M.G. Jones, Botany Department, Royal Holloway College, Egham, Surrey, U.K. |
| 75-94 | E. bicolor | Tareke Berhe, Shoa (Shewa), Debra Zeit Experimental Station, Ethiopia |
| 75-114 | E. botryodes | Dr. B.M.G. Jones, Botany Department, Royal Holloway College, Egham, Surrey, U.K. |
| 75-18 | E. capensis | Prof. D. Morgan, University of Zambia, Lusaka, Zambia |
| 75-152 | E. chapelieri | Prof. D. Morgan, University Of Zambia, Lusaka, Zambia |
| 75-167 | " | Horto Botanico, Universidade Edwardo Mondlane, Mozambique |
| 75-137 | E. cilianensis | Hortus Botanicus, Coimbra, Portugal |

| | | |
|---|---|---|
| 75-140 | " | Botanical Supply Unit, Egham, Surrey, U.K. |
| 75-168 | " | Horto Botanico, Universidade Edwardo Mondlane, Mozambique |
| 75-109 | " | Dr. B.M.G. Jones, Botany Department, Royal Holloway Collge, Egham, Surrey, U.K. |
| 78-5 | " | Jardin Botaniqe de Bordeaux, France |
| 75-125 | E. ciliaris | Dr. E.A.A. Dradu, Serere Research Station, Saroti, Uganda |
| 75-169 | " | Horto Botanico, Universidade Edwardo Mondlane, Mozambique |
| 75-145 | E. congesta | Royal Botanic Garden, Kew, Richmond, U.K. |
| 75-72 | E. curvula | Botanischer Garten und botanisches Museum, Berlin - Dahlem, Germany |
| 75-73 | " | Botanischer Garten, Munchen - Nymphenberg, Gemany |
| 75-95a | " | Dr. Tareke Berhe, Debra Zeit Experimental Station, Shoa (Shewa), Ethiopia |
| 75-64 | E.gangetica | Dr. P. Leeuw, Shika Research Station, (via Prof. B.J. Harris, Botany Department, Ahmedo Bello University, Zaria), Nigeria |
| 75-78 | " | Dr. N.H.A. Cole, Fourah Bay College, University of Sierra Leone, Freetown, Sierra Leone |
| 75-170 | E. heteromera | Horto Botanico, Universidade Edwardo Mondlane, Mozambiqe |

| | | |
|---|---|---|
| 75-107 | E. kiwuensis | Dr. B.M.G. Jones, Botany Department, Royal Holloway College, Egham, Surrey, U.K. |
| 75-19 | E. lehmanniana | United State Department of Agriculture, Texas Plant Material Centre, USA |
| 75-70 | E. mexicana | Hortus Botanicus, University of Oslo, Oslo, Norway |
| 75-74 | " | Botanischer Garten und botanisches Museum, Berlin - Dahlem, Germany |
| 75-75 | E. minor | Botanischer Garten und botanisches Museum, Berlin - Dahlem, Germany |
| 75-134 | " | Dr. B.M.G. Jones, Botany Department, Royal Holloway College, Egham, Surrey, U.K. |
| 75-69a | " | Hortus Botanicus, Acad. Sci, A.S.S.R., Armenia, Erevan, U.S.S.R. |
| 75-88 | " | Hortus Botanicus, Acad. Sci. Uz. S.S.R., Tashkent, U.S.S.R. |
| 78-6 | " | Jardin Botanique de Bordeaux, France |
| 78-7 | " | Jardin Botanique de Bordeaux, France |
| 75-65 | E. namaquensis var. diplachnoides | Dr. P. Leeuw, Shika Research Station, (via Prof. B.J. Harris, Botany Department, Ahmedo Bello University,Zaria ), Nigeria |
| 75-161 | " | Botany Department, University of Legon, Accra, Ghana |

| | | |
|---|---|---|
| 78-9 | E. orcuttiana | Jardin Botanique de Bordeaux, France |
| 75-113 | E. papposa | Dr. B.M.G. Jones, Botany Department, Royal Holloway College, Egham, Surrey, U.K. |
| 75-147 | E. patens | Royal Botanical Garden, Kew, Richmond, U.K. |
| 75-141 | E. pectinacea | Hortus Botanicus, Vacratot, Hungary |
| 78-10 | " | Jardin Botanique de Bordeaux, France |
| 75-136 | E. pilosa | Hortus Botanicus, Coimbra, Portugal |
| 75-163 | " | Hortus Botanicus, Acad.Sci. A.S.S.R., Armenia, Erevan, U.S.S.R. |
| 75-95b | E. plana | Dr. Tareke Berhe, Debra Zeit Experimental Station, Shoa (Shewa), Ethiopia |
| 75-130a | E. porosa | Dr. R.P. Denny, Matopos Research Station, Bulawaya, Zimbabwe |
| 75-124 | E. racemosa | Dr. A.A. Dradu, Serere Research Station, Sorati, Uganda |
| 75-130b | E. rigidior | Dr. R.P. Denny, Matopos Research Station, Bulawaya, Zimbabwe |
| 75-108 | E. schweinfurthii | Dr. B.M.G. Jones, Botany Department, Royal Holloway College, Egham, Surrey, U. K. |
| 75-85 | E. squamata | Dr. N.H.A. Cole, Fourah Bay College, University of Sierra Leone, Freetown, Sierra Leone |

| | | |
|---|---|---|
| 75-128 | E. superba | Dr. E.A.A. Dradu, Serere Research Station, Sorati, Uganda |
| 75-159 | " | Botany Department, University of Ghana, Legon, Accra, Ghana |
| 75-173 | " | Horto Botanico, Universidade Edwardo Mondlane, Mozambique |
| 75-6 | E. tef | Isabel Jones, Debra Zeit Experimental Station, Shoa (Shewa), Ethiopia |
| 75-7 | " | Isabel Jones, Debra Zeit Experimental Station, Shoa (Shewa), Ethiopia |
| 75-9 | " | Isabel Jones, Debra Zeit Experimental Station, Shoa (Shewa), Ethiopia |
| 75-12 | " | Isabel Jones, Debra Zeit Experimental Station, Shoa (Shewa), Ethiopia |
| 75-14 | " | Isabel Jones, Debra Zeit Experimental Station, Shoa (Shewa), Ethiopia |
| 75-93 | " | Dr. Tareke Berhe, Debra Zeit Experimental Station, Shoa (Shewa), Ethiopia |
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