Cytogenetic studies in the *Eragrostis curvula* Complex

T. B. VORSTER* and H. LIEBENBERG†

ABSTRACT

Cytogenetic studies were undertaken in the *Eragrostis curvula* Complex. Three plants were studied at each of 16 collecting points. The overall morphology and embryo sac development of all plants were evaluated, while the chromosome number and microsporogenesis of some of the plants were also studied. The collecting points were chosen so as to represent a variable environment extending from the bushveld to the highveld regions of the Transvaal. It was found that the embryo sac development of the plants from the bushveld and the highveld were, for all practical purposes, obligate diplosporic apomicts, whereas the transition area contained obligate as well as facultative diplosporic apomicts. The same pattern also held as far as the plant morphology, chromosome number and microsporogenesis were concerned.

RESUME

ETUDES CYTOGENETIQUES DANS LE COMPLEXE *ERAGROSTIS CURVULA*

Des études cytogenétiques ont été entreprises dans le complexe *Eragrostis curvula*. Trois plants ont été étudiés pour chacun des 17 points de récolte. La morphologie générale et le développement du sac embryonnaire ont été évalués partout, tandis que le nombre chromosomique et la microsporogenèse de certains plants ont aussi été étudiées. Les points de récolte ont été choisis de manière à représenter un milieu variable s'étendant des steppes boisées ("bushveld") aux prairies de montagnes ("highveld") du Transvaal. On a constaté que, dans les steppes comme dans les prairies, le développement du sac embryonnaire comporte obligatoirement une apomixie diplosporique, pour tout ce qu'on peut en observer; tandis que les zones de transition présentent aussi bien des apomictes diplosporiques obligatoires que des facultatifs. La même distribution s'observe aussi en ce qui concerne la morphologie de la plante, le nombre chromosomique et la microsporogenèse.

INTRODUCTION

Cytogenetic studies on *E. curvula* (Schrad.) Nees and its close relatives have made it clear that they are probably all part of a large agamic complex. The mechanism of apomixis is diplospory, as defined by Gustafsson (1946), followed by parthenogenesis (Håkansson, 1943) and pseudogamy as the main means of reproduction (Brown and Emery, 1958; Liebenberg, 1961; Liebenberg and Pienaar, 1962; Streetman, 1963; Voight, 1971; Voight and Bashaw, 1972 and Brix, 1974). This is probably the reason why the taxonomy of this complex has been so difficult to unravel.

The *E. curvula* group has a wide distribution throughout Southern Africa and the existence of polymorphism within species and intermediate types between species led De Winter (1955) to treat *E. robusta* Stapf as a synonym of *E. curvula* and to maintain *E. chloromelas* Steud. as a closely related species in what is generally known as the *E. curvula* Complex.

Unfortunately most of the cytogenetic studies undertaken on *E. curvula* and its relatives have been carried out, for understandable reasons, on those sections of the complex that are economically important in pasture breeding. Inevitably these sections might well comprise robust-growing high polyploid apomicts. This has created the impression that the complex was an old one consisting of mostly obligate apomicts. This has created the impression that the complex was an old one consisting of mostly obligate apomicts.

It was considered therefore that cytogenetic studies (especially embryo sac studies) of a naturally growing and unselected *E. curvula* Complex population might be well worth studying in an attempt to elucidate this problem.

MATERIAL

A region was selected in the Transvaal (South Africa), which included highveld, a transition area and lower bushveld. Seventeen collecting points were selected with three collections at each point in order to evaluate variation among as well as within collecting points over a reasonably varied area (Fig. 1).

Collecting points were selected at regular intervals on the lower bushveld and highveld, while those over the transition area were selected (with the help of Fig. 2) so that the bottom, slopes and summits of ridges would be included.

Herbarium specimens of each collection were made and identified at the National Herbarium in Pretoria, where they are now housed (Table 1).

It was decided that a minimum of fifty embryo sacs should be investigated for every plant. Additional embryo sacs of a specific plant were thus sectioned or new plants were collected when this number was not available from the collected material. More plants were therefore collected than were actually used in the study. All plants collected are reflected in Table 1 and given herbarium numbers. Those plants used in this study were, however, given additional numbers (Plant Numbers—Table 1) to identify those plants originating from one collecting point.

METHODS

The inflorescences for microtome studies were fixed in Navashin fixative (Stockholm modification—Maheshwari, 1939). Inembedding and staining techniques outlined in Johansen (1940) were followed using Heidenheins Haematoxylin as nuclear stain and Orange G as counter stain.

The propionic carmine squash method of Pienaar (1955) was slightly modified for the study of microsporogenesis and chromosome numbers.

RESULTS

Although the study of embryo sac development was the main object of the present work, microsporogenesis and chromosome numbers were also investigated as far as possible. One big problem was that by the time that microsporogenesis could be investigated (only after the embryo sacs were studied), the material had been left in the fixative too long.
Fig. 1.—Map of the roads between Brits and Johannesburg indicating the collecting points A to Q as well as the distance in kilometres between them; collecting points A to E are defined as the lower bushveld, F to M as the transition area and N to Q as the highveld.

Fig. 2.—A graph indicating the collecting points with regard to the height above sea level and distance.
Fig. 3.—Microsporogenesis stages of some of the collections. A: Diakineses of a rather “regular” tetraploid with a few distinct heteromorphic bivalents (H) — collection L-3. B: Anaphase I of a rather “regular” hexaploid — collection H-2. C: Anaphase I of a rather “regular” hexaploid (two laggards with one undergoing chromatid segregation) as well as one paracentric inversion bridge (P) — collection J-1. D: Anaphase I of a very abnormal hexaploid (approximately 12 laggards, some of them undergoing chromatid segregation, can be seen) — collection G-3.
Because of the small and compact spikelets of *Eragrostis*, fixative penetration is poor with the result that the material deteriorates soon after fixation.

Analyses were made of the number of monovalents and laggards during metaphase I and anaphase I respectively and are recorded with the chromosome numbers in Table 2. The quality of the slides did not permit multivalent or any other more complex analyses.

Paracentric inversion bridges (Fig. 3C) were also encountered in collections C-2, C-3, H-3 and J-1. These bridges, however, occurred at a very low frequency (except for plant J-1 which had chromatid bridges in 16% of the anaphase I cells studied). Apart from indicating that the polyploids are probably segmental-allopolyploids, this information was considered too scanty to be of any further use. Another phenomenon that was conspicuous in a few collections, e.g. L-3, and that would support the segmental-allopolyploid nature of the plants was the occurrence of heteromorphic bivalents, where one chromosome was much larger than its partner (Fig. 3A).

The meiotic analysis showed that plants with low chromosome numbers tend to have "regular" meioses, whereas higher polyploids were inclined to have abnormal meioses although some variation occurred. A few groups could roughly be distinguished as regard chromosome number, microsporogenesis abnormalities and the locality from whence they came:

1. Hexaploids with abnormal meioses (all these plants are from the lower bushveld and the beginning of the transition area) (Fig. 3D).
2. Hexaploids with rather "regular" meioses (these plants are from the transition area and the beginning of the highveld) (Fig. 3B).
3. An octoploid with a relative "regular" meiosis (from the transition area).
4. A pentaploid with, as expected, a very abnormal meiosis (from the transition area).
5. Two tetraploids with relatively "regular" meioses (from the transition area).

A total of 3902 embryo sacs was examined and the results are summarized in Table 1. It was found that 3306 of these embryo sacs were normal (Table 1) and only 1950 embryo sacs. One hundred and nineteen embryo sacs were abnormal or divergent, while 378 were degenerated (Table 1).

**DISCUSSION**

Four factors were considered in attempting to evaluate the natural variation in the *E. curvula* Complex in the area of this study.

1. **Morphological variation in collected material**

   It was quite striking that only true *E. curvula* was collected on the lower bushveld as well as the highveld, while true *E. curvula* as well as types which could not be judged as true were collected in the transition area (Table 1). All the *E. chloromelas* types (true and not true types) were collected in the transition area. This indicates a great deal of variation, not only between, but also within collection points in the transition area.

2. **Variation in chromosome numbers**

   The *E. curvula* Complex has a wide range of chromosome numbers, i.e. 2n = 20, 40 and 60 (Pienaar, 1953) and 2n = 50 (De Wet, 1954) for *E. curvula*, 2n = 40 and 60–63 (Pienaar, 1953) for *E. chloromelas* and 2n = 70 and 80 (Pienaar, 1953) for *E. robusta*. In this study an additional number of 2n = 80 was found for *E. curvula* in the transition area (Table 1, plant H-3).

   Although chromosome counts for only a few plants were made, it is clear that the numbers in the transition area are very variable (2n = 40, 50, 60 and 80). The few plants in the lower bushveld and highveld, which were studied in this respect, all had 60 chromosomes and, although it is risky to draw any definite conclusions, it seems as if there might be a greater chromosome number variation in the transition area.

3. **Variation in microsporogenesis**

   Table 2 shows clearly that the meioses of plants are inclined to become more regular as the transition area is approached from the lower bushveld. The two hexaploids on the highveld have rather "regular" meioses, but it would again be dangerous to draw any conclusions as to the significance of this phenomenon, because of the low number of plants investigated.

4. **Variation in embryo sac development**

   Considerable difficulty was at first experienced with the classification of some of the sexual embryo sacs and, because it was important to calculate the exact degree of sexuality for every plant, this problem has been attended to in some detail (Vorster & Liebenberg, in press).

   Sexual embryo sacs were sporadically found over the whole sampling area but they occurred at a higher frequency in the transition area (Table 1). Not only was there variation in the embryo sac development over the area as a whole, but also within collecting points.

   This occurrence of a high percentage sexuality and obligate apomixis within one collecting point stresses the discontinuous variation that occurs in the embryo sac development of the complex.

**CONCLUSIONS**

The method used in this study to try and evaluate the natural variation in embryo sac development in a specific area, proved to be very satisfactory, especially because it showed that previous studies did not reflect a true picture of the occurrence of sexuality in this complex. It would seem that the group is far from being an old obligate agamic complex. Since several specimens in the transitional zone were *E. chloromelas* types and showed, together with one *E. curvula* type, fairly high sexuality, it may be that *E. chloromelas* is supplying the source of sexuality in this area.

Sexual embryo sacs occurred most frequently in the transition area. Microsporogenesis studies showed, furthermore, that the meioses were inclined to become more regular as the transition area was approached from the lower bushveld, while the transition area also contained plants with the most variable morphology as well as the most variable chromosome numbers.

From these results, one seems justified in expecting that one or more of the original sexual ancestors of this agamic complex may still be present in or near the transition area (east or west from it) as sampled by this study. According to Stebbins (1950) the variation pattern in the *Crepis* Complex indicated that in the vicinity of diploid sexual ancestors, variable facultative apomicts occurred, whereas obligate apomicts with great morphological uniformity
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## TABLE 2 - Analysis of the average number and frequency of laggards

<table>
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<th>Plant number</th>
<th>2n</th>
<th>Average number metaphase I monovalents</th>
<th>Average number anaphase I laggards</th>
<th>Cell frequency for the different monovalents/ laggards numbers</th>
<th>metaphase I anaphase I</th>
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</table>

Diakinesis monovalents

X
were found far from them. The diploid *E. curvula* reported by Pienaar (1953) as well as the diploid sexual found by Voight (1971) in the variety *conferta* lends further evidence that at least some of the diploid sexual ancestors of the complex still exist.

In conclusion, it is clear from this study, however limited its scope, that the *E. curvula* Complex is inadequately known and understood. If any sense is to be made out of its problematic morphological variation pattern, it is clear that a complete cytogenetic study is called for. Such a study should include all related types and even species, over as much of their distribution area as possible. The present authors have already begun this task and it is hoped that in this way the relationships and therefore the taxonomy of the complex will be unravelled or at least better understood.

**REFERENCES**


**UITTREKSEL**

Sitogenetiese studies is onderneem op die *Eragrostis curvula* kompleks. Daar is drie plante by elk van die 17 versamelpunte geneem en bestudeer. Hierdie plante is geëvalueer ten opsigte van hul klassifikasie (morfologie) en kiemsakontwikkeling. Sommige van die plante se mikrosporogeenese en chromosoomaantal kon ook bestudeer word. Die versamelpunte is uitgekiets om 'n variabele omgewing, wat strek vanaf 'n laerliggende bosveld na die hoeveld, te verteenwoordig. Dit is gevind dat die kiemsakontwikkeling van die plante afkomstig vanaf die laerliggende bosveld sowel as die hoeveld vir alle praktiese doeleindes verpligte diplosporiese apomikte is, terwyl die plante afkomstig vanaf die oorgangsgebied verpligte sowel as fakultatiewe diplosporiese apomikte opgelever het. Dieselfde patroon kon waargeneem word ten opsigte van die plantmorfologie, chromosoomaantal en mikrosporogeenese.