Bothalia 32,1: 123–126 (2002)

Miscellaneous notes

POACEAE

CHROMOSOME STUDIES ON AFRICAN PLANTS. 16. POLYPLOIDY IN THE GENUS *EHRHARTA*

The genus *Ehrharta* Thunb. comprises ± 36 species of which 20 are endemic to the winter rainfall area of South Africa (Verboom 2000). The genus belongs to the tribe Ehrharteae, which has been shuffled between the Phalarideae and the Oryzeae, the Ehrharteae and Arundineae of the Arundinoideae, the Ehrharteae of the Oryzoideae, and the Ehrharteae and the Oryzaneae of the Bambusoideae (Gibbs Russell & Ellis 1987). Recently the Ehrharteae was moved from the Arundinoideae (Renvoize 1981) to the Bambusoideae (Renvoize 1985; Watson *et al*. 1985). Linder & Ellis (1990) found no other representatives of the Bambusoideae present in the Fynbos Biome. Inclusion of the tribe Ehrharteae in the Bambusoideae rests on the presence of non-anatomical characters such as bambusoid embryos and lodicules (Renvoize 1985; Clayton & Renvoize 1986). Currently the Ehrharteae forms part of the 'BEP' clade (Bambusoideae, Ehrhartoideae and Pooideae) in grass phylogenetics (Clark *et al*. 1995).

The presence of many endemic species and the absence of any close relatives to *Ehrharta* in South Africa, may present us with some answers to the formation of polyploidy in grasses. Polyploidy is a common phenomenon among the grasses and Stebbins (1985) suggested that more than 80% of species in this family have undergone some form of polyploidy somewhere in their evolutionary history. In an attempt to determine the degree of polyploidy in South African grasses, our laboratory has studied chromosome numbers of various grasses and the results were mostly published in this series.

One of the genera that has been extensively studied, is the genus *Ehrharta*. Various chromosome number reports for the genus *Ehrharta* have been published (Avdulov 1931; Nakamori 1933; Parthasarathy 1939; Löve 1948; Stebbins 1949; Raven *et al*. 1965; Tateoka 1965; Fernandes & Queiros 1969; Stebbins 1985; Spies & Du Plessis 1986; Hoshino & Davidse 1988; Spies & Voges 1988; Spies *et al*. 1989). This report includes additional results from collections from 37 populations, representing nine different species or subspecies and includes first counts for three species and one subspecies. These new counts are combined with the published results (in total more than 100 specimens have been studied) in an attempt to determine the degree of polyploidy within this genus.

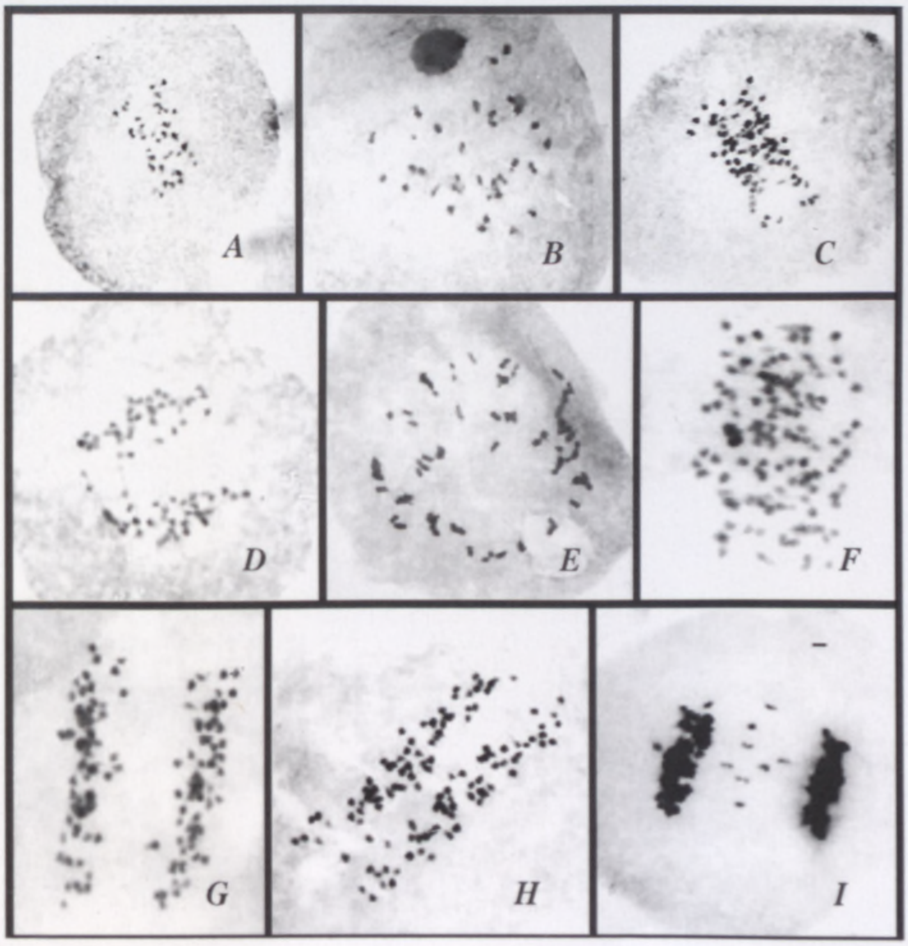

FIGURE 1.—Meiotic chromosomes in *Ehrharta*. A, *E. longifolia*, *Spies 6157*, 2n = 3x = 36, early anaphase I with a 15-21 segregation of chromosomes and even some chromatid segregation. B–D, *E. thunbergii*, *Spies 6031*, 2n = 6x = 72: B, diakinesis and early anaphase I with 36 chromosomes segregating towards each pole (not all chromosomes visible on the focus plane of photo). E–I, *E. villosa* subsp. *maxima*, *Spies 6193*, 2n = 8x = 96: E, diakinesis; F–H, early anaphase I, showing ± 48 chromosomes segregating towards each pole (a few cases of chromatid segregation can be observed and all chromosomes are not visible on this focus plane); I, late anaphase I, showing several laggards. Scale bar for A–I: 6.5 µm.

TABLE 1.—Gametic chromosome numbers of representatives of the genus *Ehrharta* (Poaceae) in southern Africa with their voucher specimen numbers and specific localities or a reference to the publication where the chromosome number was described. Species are listed alphabetically under the species groups of Gibbs Russell & Ellis (1987) and the localities are presented according to the system described by Edwards & Leistner (1971)

Taxon	n	Voucher no.	Locality or reference
Calycina Group			
E. brevifolia Schrad. var. *brevifolia*	12		Spies *et al.* (1989).
E. brevifolia Schrad. var. *cuspidata* Nees	12+0-1B		Spies *et al.* (1989).
E. calycina J.E.Sm.	12	*Spies 5937, 5938*	NORTHERN CAPE.—2917 (Springbok): 5 km from Kamieskroon to Leliehoek in the Kamiesberg Pass, (–DB).
		Spies 5950, 5952, 5953	NORTHERN CAPE.—2917 (Springbok): 8 km from Kamieskroon to Leliehoek on top of Kamiesberg Pass, (–DB).
		Spies 6043	NORTHERN CAPE.—3119 (Calvinia): 77 km from Clanwilliam to Nieuwoudtville, (–CB).
		Spies 5975	WESTERN CAPE.—3118 (Vanrhynsdorp): 8 km from Doring Bay to Lambert's Bay, (–CD).
		Spies 5977	WESTERN CAPE.—3118 (Vanrhynsdorp): 17 km from Doring Bay to Lambert's Bay, (–CD).
		Spies 6038	WESTERN CAPE.—3218 (Clanwilliam): 32 km from Clanwilliam to Nieuwoudtville, (–AA).
		Spies 5984	WESTERN CAPE.—3218 (Clanwilliam): 40 km from Clanwilliam to Lambert's Bay, (–BA).
		Spies 5990, 5995	WESTERN CAPE.—3218 (Clanwilliam): 10 km from Clanwilliam to Nieuwoudtville, (–CC).
		Spies 6013	WESTERN CAPE.—3218 (Clanwilliam): 14 km from Clanwilliam to Nieuwoudtville, (–CC).
		Spies 6260, 6261, 6262, 6265	WESTERN CAPE.—3218 (Clanwilliam): near Leipoldt's grave on top of Pakhuis Pass, (–CC).
		Spies 6082, 6322, 6323, 6326;	WESTERN CAPE.—3219 (Wuppertal): 6 km from Algeria to Citrusdal on top of Nieuwoudt Pass, (–AC).
		Spies 6063, 6317	WESTERN CAPE.—3219 (Wuppertal): on top of Uitkyk Pass, (–AC).
		Spies 6253	WESTERN CAPE.—3318 (Cape Town): 3 km E from Mamre Road, (–BC).
		Spies 6211	WESTERN CAPE.—3420 (Bredasdorp): 1 km N of De Hoop Nature Reserve, (–BA).
		Spies 6156	EASTERN CAPE.—3323 (Willowmore): 13 km from Uniondale to Oudtshoorn, (–CA).
	12+0-2B		Löve (1948); Spies & Du Plessis (1986); Spies *et al.* (1989).
	24+0-2B		Parthasarathy (1939); Löve (1948); Spies & Voges (1988); Spies *et al.* (1989).
E. delicatula (Nees) Stapf	12		Spies *et al.* (1989).
E. longigluma C.E.Hubb.			Hoshino & Davidse (1988).
E. melicoides Thunb.	12		Spies *et al.* (1989).
E. pusilla Nees ex Trin.	12		Spies & Voges (1988); Spies *et al.* (1989).
Capensis Group			
E. barbinodus Nees ex Trin.	12	*Spies 6263*	NORTHERN CAPE.—3218 (Clanwilliam): near Leipoldt's grave on top of Pakhuis Pass, (–CC).
			Spies *et al.* (1989).
E. bulbosa J.E.Sm.			Uncounted.
E. capensis Thunb.	12		Spies *et al.* (1989).
E. eburnea Gibbs-Russ.			Uncounted.
E. longifolia Schrad.	12_{III}	*Spies 6157*	EASTERN CAPE.—3323 (Willowmore): 5 km from Uniondale to Oudtshoorn, (–CA).
E. ottonis Kunth ex Nees			Uncounted.
Dura Group			
E. dura Nees ex Trin.	12+0-4B		Spies *et al.* (1989).
E. microlaena Nees ex Trin.			Uncounted.
Erecta Group			
E. erecta Lam. var. *abyssinica* (Hochst.) Pilg.	12		Tateoka (1965).
E. erecta Lam. var. *erecta*	12		Avdulov (1931); Parthasarathy (1939); Stebbins (1949); Raven *et al.* (1965); Fernandes & Queiros (1969); Stebbins (1985); Spies & Du Plessis (1986); Hoshino & Davidse (1988); Spies *et al.* (1989).
	24		Nakamori (1933); Stebbins (1949, 1985); Spies & Du Plessis (1986).
E. erecta Lam. var. *natalensis* Stapf	12		Spies *et al.* (1989).
E. longiflora J.E.Sm.	12	*Spies 6325*	WESTERN CAPE.—3219 (Wuppertal): on top of Nieuwoudts Pass, (–AC).
	12		Spies *et al.* (1989).
	24		Parthasarathy (1939); Spies *et al.* (1989).
E. triandra Nees ex Trin.	12		Spies *et al.* (1989).
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Ramosa Group			
E. ramosa (Thunb.) Thunb. subsp. *aphylla* (Schrad.) Gibbs-Russ.	12	*Spies 6319*	WESTERN CAPE.—3219 (Wuppertal): on top of Uitkyk Pass, (–AC).
		Spies 6167, 6168	WESTERN CAPE.—3322 (Oudtshoorn): Swartberg Pass, (–AC).
		Spies 6233	WESTERN CAPE.—3419 (Caledon): Galgeberg, (–BA).

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Taxon	n	Voucher no.	Locality or reference
E. ramosa subsp. *ramosa*	12	*Spies 6180*	WESTERN CAPE.—3322 (Oudtshoorn): Robinson's Pass, (–CC).
	12		Spies *et al.* (1989).
E. rehmannii Stapf subsp. *filiformis* (Stapf) Gibbs-Russ.			Uncounted.
E. rehmannii subsp. *rehmannii*	12	*Spies 6161*	WESTERN CAPE.—3322 (Oudtshoorn): Montagu Pass, (–CD).
	12+0-5B		Spies *et al.* (1989).
E. rehmannii subsp. *subspicata* (Stapf) Gibbs-Russ.	36		Spies *et al.* (1989).
Setacea Group			
E. rupestris Nees ex Trin. subsp. *dodii* (Stapf) Gibbs-Russ.			Uncounted.
E. rupestris subsp. *rupestris*			Uncounted.
E. rupestris subsp. *tricostata* (Stapf) Gibbs-Russ.			Uncounted.
E. setacea Nees subsp. *disticha* Gibbs-Russ.			Uncounted.
E. setacea subsp. *scabra* (Stapf) Gibbs-Russ.			Uncounted.
E. setacea subsp. *setacea*			Uncounted.
E. setacea subsp. *uniflora* (Burch. ex Stapf) Gibbs-Russ.			Uncounted.
Villosa Group			
E. thunbergii Gibbs-Russ.	36	*Spies 6031*	WESTERN CAPE.—3218 (Clanwilliam): 22 km from Clanwilliam to Nieuwoudtville, (–CB).
E. villosa Schult. f. var. *maxima* Stapf	48	*Spies 6193*	WESTERN CAPE.—3420 (Bredasdorp): Waenhuiskrans, (–CA).
E. villosa var. *villosa* Stapf	60		Spies *et al.* (1989).

MATERIALS AND METHODS

For this study, cytogenetic material of identical plants of a population was collected and fixed in the field. Voucher specimens listed in Table 1 are housed in the Geo Potts Herbarium, Department of Botany and Genetics, University of the Orange Free State, Bloemfontein (BLFU). The National Herbarium, Pretoria, identified the plants.

Anthers were squashed in aceto-carmine and meiotically analysed (Spies *et al.* 1996). Gametic chromosome numbers are presented for meiotic chromosomes to conform to previous work on chromosome numbers (Spies & Du Plessis 1986). Previously published somatic chromosome numbers are transformed to gametic numbers for convenience.

RESULTS AND DISCUSSION

Thirty-seven populations, representing nine species or subspecies, were studied (Table 1). All numbers support a basic chromosome number of 12 (Stebbins 1949; Spies *et al.* 1989). The majority of populations studied (93.6%) were diploid (2n = 2x = 24), with one triploid specimen, *E. longifolia*: 2n = 3x= 36 (Figure 1A); one hexaploid, *E. thunbergii*: 2n = 6x = 72 (Figure 1B–D); and one octoploid, *E. villosa* var. *maxima*: 2n = 8x = 96 (Figure 1E–I). *Ehrharta longifolia* is, to the best of our knowledge, the first triploid *Ehrharta* sample ever observed. Meiosis in this specimen was usually abnormal with numerous univalents, chromatid segregation during anaphase I, chromosome/chromatid laggards and micronuclei present. This is unfortunately the first chromosome count for this species and more individuals from more populations of this species should be investigated to determine the real chromosome number of this species.

In addition to our count for *E. longifolia*, we also report the first counts for *E. ramosa* subsp. *aphylla* (2n = 2x = 24), *E. thunbergii* (2n = 6x = 72) and *E. villosa* var. *maxima* (2n = 8x = 96). When all chromosome numbers are compared, two interesting phenomena emerge. There are no counts for any member of the Setacea Group (in spite of numerous collections by our laboratory, no successful preparations were made) and all three counts for the Villosa Group are polyploids. Additional populations should be studied to determine whether this whole group consists of high ploidy levels and whether it represents hybrids (alloploids) between representatives of other groups.

The majority of populations studied (more than 97%) suggest a basic chromosome number of x = 12 for *Ehrharta*. However, basic chromosome numbers higher than nine are secondarily derived basic numbers (Goldblatt 1980). It is also well known that most bambusoids have a secondary basic chromosome number of 12 (Stebbins 1985). Stebbins (1985) suggested that polyploidy follows one of four different ways in grasses. *Ehrharta* forms part of Stebbins' third mode of polyploidy—'multiples of a basic number that is the lowest in its genus, but was probably derived from that of pre-existing genera by a cycle of polyploidy in the remote past'. An example of this mode is given as *Leersia* Sw., another member of the Bambusoideae (Stebbins 1985). The genus *Ehrharta* is consequently of ancient polyploid origin and the basic chromosome number of x = 12 can be described as a secondary basic chromosome number.

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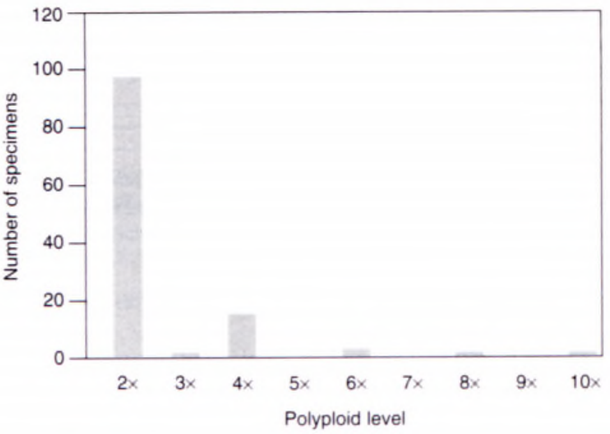

FIGURE 2.—Number of specimens per ploidy level for all *Ehrharta* specimens studied.

This paper began by mentioning that more than 80% of grasses are polyploids; the question remains whether the initial polyploidization of the basic chromosome number in *Ehrharta* enhanced or inhibited further polyploidization events. All chromosome numbers observed for *Ehrharta* populations indicate that 82.8% are 'diploid' (Figure 2). This dramatic decrease from 80% polyploidy in grasses to more than 80% diploidy in *Ehrharta* indicates that the initial polyploidization event probably inhibited the consequent formation of polyploidy in the genus. However, the frequency of polyploidy varies in different taxa and this conclusion should be studied further in order to determine whether the decrease in secondary polyploidization is a general phenomenon or specific to the genus *Ehrharta*. The influence of climatic and geographical factors on polyploidization is not fully understood, therefore, we did not compare these results with chromosome numbers of other bambusoids, since no other bambusoids grow sympatrically with *Ehrharta*.

ACKNOWLEDGEMENTS

Financial assistance given by the University of the Orange Free State and the National Research Foundation is gratefully acknowledged.

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MS. received: 2001-03-23.