Estella Nazarova

Chromosomal polymorphism in Armenian population of *Crepis pannonica (Asteraceae)*

Abstract

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A population of *Crepis pannonica,* growing in the Hosrov reserve in Armenia, at the southern limit of the species' area, has been investigated over a period of more than 20 years. An extraordinary chromosomal polymorphism has been detected by the study of root tip mitoses of seedlings. 40 different chromosome complement variants were found, including a full range of aneuploids, B-chromosomes, structural hetero- and homozygotes, witnessing active chromosomal restructuring and karyotype evolution.

Introduction

Crepis pannonica (Jacq.) K. Koch is a perennial cross-pollinating species ranging from Central Europe to West Siberia. Its karyotype formula is $2n = 8 =$ AA (SM) + BB (SA) + CC (SM) + DD (A^S) (Nazarova 1976, see also Babcock 1947).

We have been investigating the Hosrov reserve population of *Crepis pannonica,* in Central Armenia, for over 20 years. Being situated at the southernmost edge of the vast area of the species, this population attracted our attention because of its unusual karyological polymorphism. Throughout our investigations we did not find a single plant whose seed progeny was completely exempt of deviations in karyological features. In some years (1973, 1978, and 1984) the population was totally seed-sterile in spite of abundant flowering. In the other years, both sterile plants and plants with reduced fertility (from 1.8 % to 78.3 % of germinating seeds) were found. Obviously, the generative reproduction of *C. pannonica* in this population is very depressed.

Materials and methods

Seed from 30 plants was gathered each year in September. Seed number, germination rate, and chromosomal variation were recorded separately for each individual progeny.

Mitotic metaphases of root tips of a total number of 3544 seedlings were examined using standard Feulgen squash technique as detailed in Nazarova (1994).

Table 1. The variation of chromosome number (*2n*), autosome complement, and B chromosome number in progeny of an Armenian population of *Crepis pannonica*.

2*n*	Autosome complement				B chromos.	Seedlings
8	AA	BB	CC	DD	0	2149
	AA	BB	CC	DD	1	875
	AA	BB	CC	DD	2	252
	AA	BB	CC	DD	3	64
	AA	BB	CC	DD	4	12
	AA	BB	CC	DD	6	1
9	AAA	BB	CC	DD	0	11
	AA	BBB	CC	DD	0	4
	AA	BB	CC	DDD	0	9
	AAA	BB	CC	DD	1	3
	AA	BBB	CC	DD	1	2
	AAA	BB	CC	DD	2	3
10	AAA	BBB	CC	DD	0	4
	AAA	BB	CC	DDD	0	2
	AA	BBB	CCC	DD	0	1
	AA	BBB	CC	DDD	0	2
	AAA	BBB	CC	DD	1	6
	AAA	BBB	CC	DD	2	1
	AAA	BB	CC	DDD	2	1
	AAA	BBB	CC	DD	3	1
	AAA	BB	CC	DDD	3	1
11	AAA	BBB	CCC	DD	0	10
	AAA	BBBB	CC	DD	0	1
	AAA	BBB	CC	DDD	0	6
	AAA	BB	CCC	DDD	0	7
	AAA	BB	CCCC	DD	0	1
	AA	BBB	CCC	DDD	0	3
	AAA	BB	CCC	DDD	1	3
	AA	BBB	CCC	DDD	1	2
	AAA	BBB	CCC	DD	2	2
	AAA	BBB	CCC	DD	3	1
12	AAA	BBB	CCC	DDD	0	67
	AAA	BBB	CCC	DDD	1	21
	AAA	BBB	CCC	DDD	2	6
	AAA	BBB	CCC	DDD	3	3
	AAA	BBB	CCC	DDD	4	1
13	AAAA	BBB	CCC	DDD	3	1
14	AAA	BBB	CCC	DDDDD	1	1
15	AAAA	BBBB	CCCC	DDD	1	1
	AAAA	BBBB	CCC	DDD	4	1
16	AAAA	BBBB	CCCC	DDDD	0	2

Results

The observed types of chromosome complements and their frequency are summarised in Table 1. In all, 40 different karyotype variants have been observed, among which the standard type ($2n = 8 + 0$ B-chromosomes; Fig. 1) predominates. The somatic chromosome number ranged from 8 to 16 owing to occasional tri- or tetrasomy (in one case, pentasomy).

The number of B-chromosomes (Fig. 2-4) varied from 0 to 6. Polymorphism in these accessory chromosomes has also been found. Besides the standard type of B chromosomes, three derivative types have been observed: small acrocentric ones (Fig. 5), isochromosomes, and submetacentric satellited ones.

In addition to numerical polymorphism of autosomes and B-chromosomes, numerous structural rearrangements were observed in the Hosrov population of *Crepis pannonica*. In some cells there were multiple rearrangements, sometimes involving most or all chromosomes of the set, and it was difficult to identify them. Di- and polycentric chromosomes were observed, and in the cytoplasm there were large and small chromatin lumps. In the interphase stage, micronuclei of varying number and size were visible. When the rearrangements were so profound, the seedlings would perish.

Investigation of microsporo- and microgametogenesis (the details of which will be reported elsewhere) supported the identification of structural mutations of chromosomes. Rearrangements (deletions, inversions, and translocations) often affect one or two chromosomes of the set. Specimens with an altered (heterozygous) karyotype appeared in the progeny of plants with a normal karyotype. Observed structural mutations include inter- and intrachromosomal translocations (A-D, A-B, C-C, B-C), deletions in the C and D chromosome, and an inversion in the D chromosome (Fig. 6).

Usually all such rearrangements are unique, i.e., the heterozygous individuals in which they appear will perish. The single exception was a rearrangement that we identified as a pericentric inversion in the A chromosome (Fig. 7), which was observed in the heterozygous state among the seed progeny of 5 different plants. 49 out of a total of 324 seedlings of their progeny (15 %) showed that inversion in one of their A chromosomes. Such a high frequency, when none of the mother plants showed the same anomaly, is best explained by the assumption that one or several plants with this rearrangement in the homozygous state occur in the population, providing whole loads of pollen with an altered karyotype.

Discussion

Progeny from the Hosrov population of *Crepis pannonica* included a predominance (94.6 %) of diploids, fairly frequent (2.8 %) triploids, and exceptional (0.06 %) tetraploids. Aneuploid chromosome numbers are mostly observed among the progeny of triploid plants. Trivalent formation in the meiosis of triploids causes various disturbances during chromosome disjunction and results in the presence of gametes with an unbalanced chromosome number. We therefore find plants with a single trisomy and a chromosome number of $2n = 9$, or a double trisomy ($2n = 10$), or treble trisomy ($2n = 11$), or with a single or multiple tetrasomy and with chromosome numbers of $2n = 11$, 13, 14, or 15. Appearance of aneuploids ($2n = 9$, 10, 11, 13, 14 and 15) in the progeny of diploids is also of note.

The Hosrov population is further characterised by a high frequency of B-chromosomes. The same standard type of B-chromosomes as in the Armenian *Crepis pannonica* population has been observed a in widely separate population, in Hungary (Fröst 1960). This suggests a common origin.

The occurrence of B-chromosomes must be viewed against the background of the population's whole chromosomal polymorphism: variation of autosome numbers (aneuploidiy

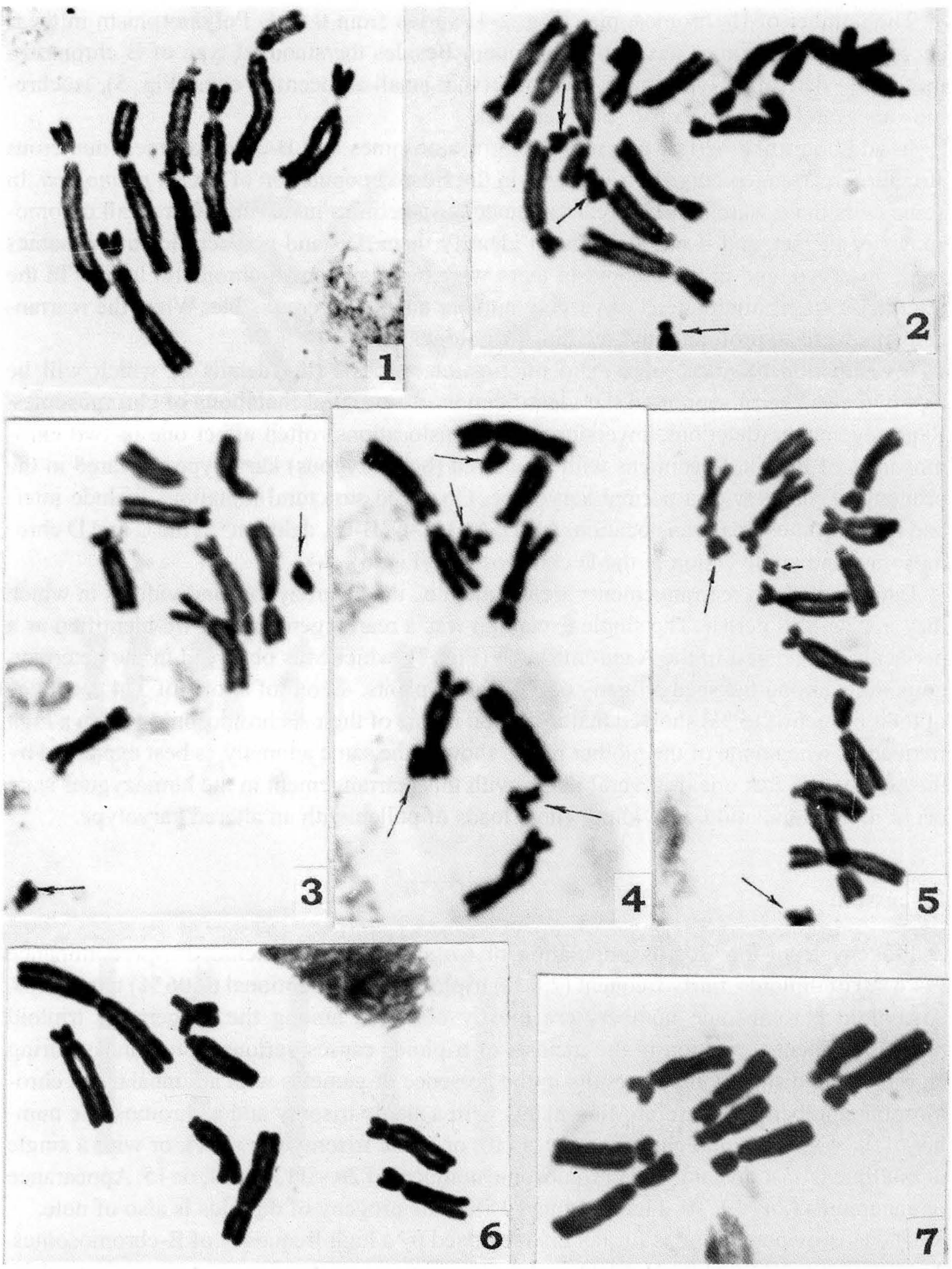

Fig. 1-7. Somatic metaphase plates from seedling root tips of Armenian *Crepis pannonica*. – 1, standard diploid type ($2n = 8$); 2, type with $2n = 13$ chromosomes (AAAA + BBB + CCC + DDD + 3B [arrows]); 3, diploid ($2n = 8 + 2B$ [arrows]); 4, diploid ($2n = 8 + 4B$ [arrows]); 5, triploid ($2n = 12 + 2B$ [standard; arrows] + 1B [deviating, small acrocentric; short arrow]); 6, diploid ($2n = 8$) with one A-B translocation; 7, diploid ($2n = 8$) with pericentric inversion in one A chromosome.

and polyploidy), structural rearrangements, heterochromatin variation, and satellite DNA. The analysis of our results, which reflect the investigations of many years, stresses the need to consider B-chromosomes, not in isolation but in the full context of karyotypical characteristics of the population in which they are found. In addition to the root tip mitotic data reported here, which demonstrate numerical variation of B-chromosomes in the progeny of single plants and within the whole population, the study of microsporo- and microgametogenesis has unveiled the mechanisms of B-chromosome variation (Nazarova 1976).

Polymorphism in structural rearrangements is not rare in nature and has been recorded for numerous species of flowering plants. Chromosomal mutations appearing spontaneously in natural populations are active speciation factors (Dubinin & al. 1965, Grant 1981). Species, and discrete populations in different parts of the area of a species, show varying mutation ability.

Work on *Trillium grandiflorum* (Rutishauser 1956, 1960), *Ornithogalum umellatum* (Neves 1952, Giménez-Martín 1958, Czapik 1967), *Ranunculus ficaria* (Marchant & Brighton 1974), *Pterocarya falconeri* (Kausal & Mehra 1976), *Zebrina pendula* (Armando 1984), etc. has produced many interesting examples of spontaneous karyological polymorphism of populations with respect to B-chromosomes. Most of these investigations emphasise the influence of B-chromosomes on the autosome complement, mentioning for example that when accessory chromosomes are present the frequency of autosome mutations and aneuploidy increases. In other words, the karyotype polymorphism of populations is considered to be due to the occurrence of B-chromosomes. We believe that the reverse is true: a high level of natural mutation of the autosome complement, in a given population, will cause the presence of B-chromosomes (Nazarova 1976, 1988). They appear as centric fragments during structural rearrangements leading to a reduction of the basic chromosome number, and remain in the population due to their having a centromere. They can be lost through numerous generations in the process of evolution.

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Address of the author:
Dr E. Nazarova, Institute of Botany of the Armenian National Academy of Sciences,
375063 Erevan, Armenia.