ISOENZYMATIC AND CYTOLOGICAL STUDIES OF SOME ASIATIC SPECIES OF THE GENUS *SALSOLA*

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(Received: October 15, 2001. Accepted: March 13, 2002)

ABSTRACT

The genetic and cytological variability of population of three *Salsola* species from Asia was investigated, using isozyme electrophoresis and haematoxylin staining. Eight enzyme systems, representing 14-17 loci, were examined: 6PGD, DIA, G6PD, GDH, GOT, MDH, PGM and PGI. Analysis of the chromosome number revealed that the three species have the same number of chromosomes: $2n=18$. Parameters describing genetic diversity indicate a very low level of genetic variation of the studied populations. The isozyme data support hypothesis that strong directional selection can result in lower level of genetic variation of arid plant populations.

KEY WORDS: *Salsola* species; isoenzymes; genetic diversity; chromosome number.

INTRODUCTION

More than 120 species (Botschantsev 1969; Freitag 1996) of the genus *Salsola* (Chenopodiaceae) are known in the flora of Central Asia. The genus includes shrubs, subshrubs and herbs both perennial and annual. In the flora of Uzbekistan *Salsola* spp. account for up to 45% of the species of the family Chenopodiaceae; they are found in typical deserts and semideserts, and are very important ecologically in saline and arid areas of the Kyzyl-Kum Desert. Dryland plants, and *Salsola* species in particular, provide a potential model for studies of reproductive strategies, morpho-anatomical traits and population genetic structures associated with tolerance to drought and salt. Many taxa of this group are considered to be useful for rehabilitation of degraded and salt-affected land. These xerohalophytic species have a high economic value as pasture plants on saline land, and are readily eaten by animals, especially in autumn and winter. In addition to their biomass production, many species of Asiatic *Salsola* spp. can be used as a material for medicinal and industrial purposes.

The extremely high morphological variability of the annual species of *Salsola* section *Salsola* (*Kali* Ulbrich) has been known for a long time and has led to the description of several species, subspecies and varieties (Ulbrich

1934; Prator 1986). The biogeographical, morphological and ecophysiological characteristic of species belonging to this section have also been studied in relation to their systematic position (Butnik 1984; Rilke and Reimann 1996; Li et al. 2000). The genetic variation of *Salsola* spp. within their native ranges in Europe and Asia is not well known (Ryan and Ayres 2000) as well as other plants from arid regions (Schuster et al. 1994). Another unanswered question is to what extent their great morphological variability represents genetic, developmental or environmental differences (Rilke and Reimann 1996).

The present study was conducted in an attempt to estimate the genetic variation and describe the genetic structure of populations of three annual species (*Salsola lanata* (syn. *Climacoptera lanata*), *Salsola praecox* and *Salsola pestifer*), which grow under desert and highly saline conditions of the southern Kyzyl-Kum Desert in Uzbekistan.

MATERIAL AND METHODS

Plant material

Seeds were collected from 10-15 mother plants of each species and mixed together to make the seed pool. The sample of 100 seeds from each species was randomly cho-

TABLE 1. Environment description and number of the studied individuals (n) of *Salsola* species.

Species	Localisation	Soil	Rainfall	n
<i>Salsola lanata</i>	Ecocentre "Djeýran" in the south-east Kyzyl-Kum Desert (Bukhara region)	Solonchaks, saline sandy soils	75-130 mm	26
<i>Salsola pestifer</i>	Foothills semidesert zone, about 5-8 km from Samarkand city	Clay or clay loamy, rarely salty soils	108-400 mm	32
<i>Salsola praecox</i>	Ecocentre "Djeýran" in the south-east Kyzyl-Kum (Bukhara region)	Gray-brown, small sandy hills or fixed sandy loamy soils	75-130 mm	32

sen for germination and then used for electrophoretic and cytological analysis. Description of examined plant material is given in Table 1.

In the Kyzyl-Kum Desert *Salsola lanata* forms distinct and almost monospecific communities on solonchaks and solonetz soils, on clay and gypsiferous deserts and on solonchak-alkaline soils. It flowers from July to October. *S. praecox* grows on steppes and sandy solonchaks of Central Asia: in particular in the Aral-Caspian region, Balkhash, Kyzyl-Kum, Kara Kum and Amu Darya valley. Its native populations are often small and isolated. *S. pestifer* forms steppe plant communities, rarely occurs on sands and/or on old fields as a weed and in the forest steppe and steppe belts of Europe, West Siberia and Central Asia: Balkhash, Mongolia and China. *Salsola pestifer* and *S. praecox* occur on dry, sandy soils, usually moderately saline. Both species possess a high polymorphism and morphologically are very similar to each other. The flowering period in *S. praecox* lasts from April to September, and in *S. pestifer* from July to September.

Isoenzymatic analysis

On the basis of starch gel electrophoresis of isoenzymes from randomly chosen embryos, variability of the following enzymatic systems was studied: phosphogluconate dehydrogenase (6PGD, E.C. 1.1.1.44), malate dehydrogenase (MDH, E.C. 1.1.1.37), glutamate dehydrogenase (GDH, E.C. 1.4.1.2), glucose-6-phosphate dehydrogenase (G6PD, E.C. 1.1.1.49), phosphoglucomutase (PGM, E.C. 5.4.2.2), phosphoglucoisomerase (PGI, E.C. 5.3.1.9), glutamate oxaloacetate transaminase (GOT, E.C. 2.6.1.1), NADH diaphorase (DIA, E.C. 1.6.99). Enzymes were extracted by homogenisation of a single embryo in 80 µl of extraction buffer: EDTA, KCl, MgCl₂, TRITON, PVP, TRIS-HCl. Isoenzymes were separated on 10% starch gel using two buffer systems (Muona et al. 1987; Odrzykoski and Staszak, unpub.): (1) TC: electrode buffer of Tris and citric acid, pH 8.0 with 2M Tris; gel buffer of 10 ml of electrode buffer diluted with 90 ml H₂O, pH 8.0 with 2M Tris; and (2) PK: electrode buffer of boric acid and NaOH, pH 8.2 with 4M NaOH; gel buffer of Tris and citric acid, pH 8.7 with 2M Tris. Electrophoresis was carried out for about 6-7 hours under the following conditions: TC buffer system, 90 V, 40-50 mA; PK buffer system, 210 V, 70-80 mA at 5°C. Staining of particular enzymes as well as genetic interpretation of the results followed standard techniques (Rudin and Ekberg 1978; Szmidt and Yazdani 1984; Muona and Szmidt 1985). On the basis of electrophoretic data the following parameters were calculated to describe genetic structure of the population: frequencies of alleles and genotypes, mean number of alleles and geno-

types per locus (A/L, G/L), expected and observed heterozygosity (He, Ho), Wright's fixation index (F), genotype polymorphism index (Pg), genetic distance and similarity based on alleles (Nei) and genotypes (Hedrick) frequencies (according to procedures described by Nei and Roychoudhury 1978; Nei 1972; Hedrick 1974; Sneath and Sokal 1973; Wright 1969).

Cytological analysis

At least three root apices were examined from each population. The chromosomes were counted exclusively on mitotic plates (three to five plates for each species) at metaphase or anaphase. The samples were handled according to following schedule: a) fixation in freshly mixed 3:1 absolute alcohol: glacial acetic acid, for at least 24 h in a refrigerator; b) transfer to 45% of acetic acid for a 24 h; c) root apices were cut and then macerated; d) meristem fragments were carefully heated to boiling in a drop of haematoxylin for 5-7 min; staining solution was removed with blotting paper; e) permanent preparations were made by mounting stained tissues in Euparal or in Hoyer's medium.

RESULTS

We examined eight enzyme systems, which were coded by different numbers of loci in particular species: 14 in *S. lanata*, 17 in *S. pestifer* and 16 in *S. praecox*. In the population of *S. lanata* three loci GDH B, GOT B, PGM B, that occurred in the two *Salsola* species were not observed. Locus G6PD A was found only in *S. lanata*, and locus PGI A only in *S. pestifer*. We observed a null allele in locus MDH C in *S. lanata*. The general pattern of isoenzymatic bands of *S. pestifer* and *S. praecox* were similar for all loci, except PGI A, which was observed only for *S. pestifer*. In *S. lanata*, the enzymes G6PD, PGM, GOT, GDH and PGI are coded by different numbers of loci than in *S. pestifer* and *S. praecox*. Zymograms of the all examined loci are presented in Fig. 1 as they were seen on the gels. As seen from Fig. 2, loci 6PGD and MDH of *S. lanata* clearly differ from those of *S. pestifer* and *S. praecox*. Frequencies of alleles and genotypes at particular enzyme loci are given in

Fig. 1. Zymograms of observed genotypes in particular enzymes loci.

Fig. 2. The differences in patern bands of two enzymes between *Salsola pestifer*, *Salsola praecox*, and *Salsola lanata*.

Tables 2 and 3. The proportion of polymorphic loci (at 0.99 criterion, Nei 1987) was rather low and ranged from 5.9% for *S. pestifer* and 12.5% for *S. praecox* to 21.4% for *S. lanata* (Table 4). The χ^2 test confirmed the significance of differences in allele PGI C2 and genotype PGI C 1/2 frequencies between *S. lanata* and *S. praecox* and between *S. pestifer* and *S. praecox*. Overall, 18 alleles and 18 geno-

types were found in *S. pestifer* and *S. praecox*, and 17 alleles and 17 genotypes were found in *S. lanata*.

Parameters describing genetic diversity, given in Table 4, indicate a very low level of variation of the investigated species. The mean number of alleles and genotypes per locus was very low: from 1.1 in *S. pestifer* and *S. praecox* to 1.2 in *S. lanata* for both parameters. The mean observed heterozygosity H_o (average over loci) was the highest for *S. praecox* (0.159), intermediate for *S. pestifer* (0.129) and the lowest for *S. lanata* (0.031). In all the investigated species there was a significant excess of heterozygotes (test χ^2) as indicated deviation from Hardy-Weinberg equilibrium (Table 4).

S. lanata and *S. pestifer* have similar values of genotype polymorphism index P_g (0.025 and 0.029 respectively), as opposed to *S. praecox*, which has the highest genotype polymorphism (0.054).

Values of genetic distance based on allele DN and genotype DH frequencies are summarised in Table 5. In both cases the smallest genetic distance was found for the pair *S. lanata*-*S. pestifer* and the largest for *S. pestifer*-*S. praecox*.

Chromosome number $2n=18$ was the same for three investigated species and is presented at Fig. 3.

TABLE 2. Frequencies of alleles in the studied species: S.l – *Salsola lanata*, S.p – *Salsola pestifer*, S.x – *Salsola praecox*.

Locus/allele	S.l	S.p	S.x
6PGD A			
1	1.000	1.000	1.000
6PGD B			
1	1.000	1.000	1.000
DIA A			
1	1.000	1.000	1.000
DIA B			
1	1.000	1.000	1.000
G6PD A			
1	1.000	–	–
G6PD B			
1	1.000	1.000	1.000
GDH A			
1	1.000	1.000	1.000
GDH B			
1	–	1.000	1.000
GOT A			
1	1.000	1.000	1.000
GOT B			
1	–	0.741	0.859
2	–	0.259	0.141
MDH A			
1	0.984	1.000	1.000
2	0.016	–	–
MDH B			
1	1.000	1.000	1.000
MDH C			
1	0.906	1.000	1.000
null	0.094	–	–
PGI A			
1	–	1.000	–
PGI B			
1	1.000	1.000	1.000
PGI C			
1	0.969	1.000	0.823
2	0.031	–	0.177
PGM A			
1	1.000	1.000	1.000
PGM B			
1	–	1.000	1.000

TABLE 3. Frequencies of genotypes in the studied species: S.l – *Salsola lanata*, S.p – *Salsola pestifer*, S.x – *Salsola praecox*.

Locus/genotype	S.l	S.p	S.x
6PGD A			
1/1	1.000	1.000	1.000
6PGD B			
1/1	1.000	1.000	1.000
DIA A			
1/1	1.000	1.000	1.000
DIA B			
1/1	1.000	1.000	1.000
G6PD A			
1/1	1.000	–	–
G6PD B			
1/1	1.000	1.000	1.000
GDH A			
1/1	1.000	1.000	1.000
GDH B			
1/1	–	1.000	1.000
GOT A			
1/1	1.000	1.000	1.000
GOT B			
1/1	–	0.483	0.719
1/2	–	0.517	0.281
MDH A			
1/1	0.969	1.000	1.000
1/2	0.031	–	–
MDH B			
1/1	1.000	1.000	1.000
MDH C			
1/1	0.906	1.000	1.000
null	0.094	–	–
PGI A			
1/1	–	1.000	–
PGI B			
1/1	1.000	1.000	1.000
PGI C			
1/1	0.938	1.000	0.645
1/2	0.063	–	0.355
PGM A			
1/1	1.000	1.000	1.000
PGM B			
1/1	–	1.000	1.000

TABLE 4. The main genetic parameters calculated for the studied species: A/L – mean number of alleles per locus, G/L – mean number of genotypes per locus, He – expected heterozygosity, Ho – observed heterozygosity, F – Wright’s fixation index, Pg – genotype polymorphism index.

Populations	% of loci polymorphic ¹	A/L	G/L	He	Ho	F	Pg
<i>S. lanata</i>	21.4	1.2	1.2	0.019	0.031	-0.675 ²	0.025
<i>S. pestifer</i>	5.9	1.1	1.1	0.023	0.129	-4.733 ²	0.029
<i>S. praecox</i>	12.5	1.1	1.1	0.033	0.159	-3.768 ²	0.054

¹ at 0.99 criterion, Nei 1987
² significance confirmed by χ^2

TABLE 5. Genetic distances and similarities according to Nei (below diagonal) and according to Hedrick (above diagonal) between the studied species.

	genetic distance			genetic similarities		
	<i>S. lanata</i>	<i>S. pestifer</i>	<i>S. praecox</i>	<i>S. lanata</i>	<i>S. pestifer</i>	<i>S. praecox</i>
<i>S. lanata</i>	–	0.0011	0.0076	–	0.999	0.992
<i>S. pestifer</i>	0.0007	–	0.0119	0.999	–	0.988
<i>S. praecox</i>	0.0024	0.0029	–	0.998	0.997	–

Fig. 3. Chromosome number of *Salsola pestifer*, *Salsola praecox*, and *Salsola lanata*.

DISCUSSION

As described above populations of examined three taxa show isozyme monomorphism in majority of enzyme loci (Table 2). The number of examined loci (14-17) was quite representative for estimation of populational variation, thus such a low genetic differentiation of the studied taxa is noteworthy. This fact may be a characteristic feature of the family Chenopodiaceae, as indicated by data for diploid and tetraploid *Chenopodium* species (Crawford 1979; Wilson 1981) and for *Salsola tragus* (Ryan and Ayres 2000), where high percentage of monomorphic loci are observed. Values of the calculated genetic parameters (Table 4) indicate a very low genetic diversity of the studied species. A low genetic variation was also detected in *Chenopodium* spp. by Crawford and Wilson (1979). Wilson (1988a, b) reports that wild and cultivated populations of *Chenopodium quinoa* from the Andes share a low level of allozyme variation, with no distinction between domesticated and wild populations. A low level of intraspecific variation by RAPD markers was also found within six species of this genus by Ruas et al. (1999). Contrary, high level of genetic variation was observed in four dominant arid species in Arizona: *Encelia farinosa*, *Larrea tridentata*, *Gutierrezia microcephala* and *Coleogyne*

ramosissima (Schuster et al. 1994). These species were characterised by high percentage of polymorphic loci (50-78.9%) and mean number of alleles per locus (2.0-2.28). Genetic similarities between examined species are surprisingly high: 0.997-0.999 according to Nei (IN) and 0.988-0.999 according to Hedrick (IH), especially in comparison to values given by Crawford (1983) for *Chenopodium* spp.: 0.35-0.97. Genetic similarities calculated for *S. lanata*, *S. pestifer* and *S. praecox* are as high as for conspecific populations of several *Chenopodium* species (Crawford 1983). Genetic distances between the studied taxa are much lower (0.0007-0.0029) than values estimated by Nei (1976) between species 0.1-0.2 and between subspecies 0.02-0.1. Such a high isozyme monomorphism of *Salsola* species may be due to very nar-

row environmental conditions, under which only highly specialised organisms can survive. This conclusion is in concordance with the hypothesis of Hamrick et al. (1979). The authors suggest that strong directional selection might result in lower levels of genetic variation in arid plant populations. According to Golding (1994) environment factors also shape frequencies of alleles, thus taxa experiencing similar conditions may exhibit similar allele frequencies. The above genetic data suggest that a significant component of the great morphological variation of the examined taxa may result from phenotypic plasticity. By contrast, Rilke and Reimann (1996) present that differential saline tolerance of *Salsola kali* from northern Europe suggests some genetic differentiation.

The lack of activity of the four loci in the population of *S. lanata*, as well as the presence of the unique G6PD A locus, distinguishes its genetic structure from those of *S. pestifer* and *S. praecox*. The lowest heterozygosity, Wright’s fixation index and genotype polymorphism index support this. High salinity regimes of the habitats may be responsible for the genetic distinctiveness of *S. lanata*. Despite it, a very high genetic similarity (0.999) was found between populations of *S. lanata* and *S. pestifer*. These surprising data may due to unclear systematic position of *S. lanata*. It was first described as *Salsola lanata* sec. *Eusalsola* (Ulbrich 1934) or sect. *Physurus* (Iljin 1937). Because of several unique morphological traits of leaves, flowers and fruits it was separated as a genus *Climacoptera* by Botshantsev (1969) and Prator (1986). Hedge et al. (1997) replaced this taxon again to genus *Salsola* sect. *Physurus*. From palynological poin of view Toderich et al. (2000) consider *S. lanata* as distinct species belonging to genus *Climacoptera* closely related to genus *Salsola*. What distinguishes two *Salsola* species is the lack of G6PD A locus and the presence of the polymorphic locus GOT B. The more differentiating locus for *S. praecox* seems to be PGI C, which allele and genotype frequencies were significantly different from those of the remaining two species.

In our study we found that pattern of the two 6PGD loci seems to be very similar (or the same) to the type B of Californian *S. tragus* (regarded as synonym for *S. pestifer*) described by Ryan and Ayres (2000). They suggest, on the basis of electrophoretic and cytological analysis, that two distinct isoenzymatic types (A and B) of 6PGD and GOT enzymes are in fact two different species. The number of chromosomes estimated in *S. pestifer* ($2n=18$) confirms that the investigated plants belong to the Californian type B of this species.

In conclusion, the results of this paper, as well as works of Crawford and Wilson (1977, 1979), Crawford (1983), Ryan and Ayres (2000), demonstrate the usefulness of electrophoresis for exploring the genetic diversity and taxonomic position of taxa of family Chenopodiaceae. Obviously, our findings based on the analyses of the only one population of each species, are preliminary and require further studies on wider plant material in respect to genetic variation and its relation to environmental conditions.

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IZOENZYMATYCZNA I CYTOLOGICZNA ZMIENNOŚĆ
AZJATYCKICH GATUNKÓW RODZAJU *SALSOLA*

STRESZCZENIE

Badano zmienność genetyczną i cytologiczną populacji trzech gatunków rodzaju *Salsola* z Azji. Metodą elektroforezy białek na żelu skrobiowym zanalizowano osiem systemów enzymatycznych, które kodowane były przez zmienną u poszczególnych gatunków liczbę loci (14-17). Barwienie hematoksyliną wykazało, że populacje badanych gatunków mają tę samą liczbę chromosomów wynoszącą $2n=18$. Wartości parametrów opisujących strukturę genetyczną populacji wskazują na ich bardzo niski poziom zróżnicowania genetycznego. Uzyskane dane izoenzymatyczne potwierdzają hipotezę Hamricka i współautorów, że silna selekcja kierunkowa może być przyczyną niższego poziomu zmienności genetycznej populacji roślin pustynnych.

SŁOWA KLUCZOWE: gatunki *Salsola*, izoenzymy, zróżnicowanie genetyczne, liczba chromosomów.