

Chromosome number and meiotic behaviour of two populations of *Onobrychis chorassanica* Bunge (*O. sect. Hymenobrychis*) in Iran

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Abstract

The genus *Onobrychis* belongs to family Fabaceae and has about 130 species throughout the world. *Onobrychis* sect. *Hymenobrychis* with nearly 14 species in Iran is one of the important sections of the genus. The chromosome number and meiotic behaviour were studied in two populations of *Onobrychis chorassanica* belonging to this section native to Iran. This report is the first cytogenetic analysis of this taxon. Both populations are diploid and possess $2n = 2x = 14$ chromosome number, consistent with the proposed base number of $x = 7$. Although these taxa displayed regular bivalent pairing and chromosome segregation at meiosis, some meiotic abnormalities were observed. The meiotic abnormalities included varied degrees of chromosome stickiness including B-chromosome, cytomixis, asynchronous nucleus, fragmented chromosomes, occurrence of laggard chromosomes, chromosome bridges, desynapsis, micronucleous and tripolar cells.

Keywords: chromosome number, Fabaceae, meiotic behaviour, *Onobrychis chorassanica*, *O. sect. Hymenobrychis*.

Introduction

The genus *Onobrychis* with nearly 130 species is mainly distributed in the north temperate regions, but centers of diversity are in the eastern Mediterranean area and western Asia. *Onobrychis* includes annual or perennial, mostly caulescent herbs (rarely spiny shrubs), which have an indumentum with simple hairs or rarely are glabrous. A few taxa of the genus such as *O. viciifolia* are cultivated as fodder or for ornamental value (Lock and Simpson, 1991; Mabberley, 1997; Yakovlev et al., 1996). *O. sect. Hymenobrychis* with nearly 14 species in Iran is one of the important sections of the genus. The taxonomy of the genus continues to be the subject of much confusion, mainly because of the different approaches to species delimitation, resulting in varying numbers of recognized species (Aktoklu, 2001; Ball, 1978; Boissier, 1872; Duman and Vural, 1990; Hedge, 1970; Sirjaev, 1925). Recently some new taxa of the genus have been described from Iran (Ranjbar et al., 2004, 2006, 2007a, 2007b, 2009a, 2009b, 2010c and 2010d).

Most of the cytological studies in the genus have concentrated on the chromosome count

(Baltisberger, 1991; Karshibaev, 1992; Slavivk et al., 1993), with little work focused on detailed karyological criteria for taxonomic purposes (e.g. Khatoun et al., 1991; Mesicek and Sojak, 1992). From these and other reports (e.g. Abou-el-Enain, 2002; Diaz-Lifante et al., 1996; Fedorov, 1969; Goldblatt, 1981a, 1984, 1985, 1988; Goldblatt and Johnson, 1991; Romano et al., 1987), it is evident that the chromosome count is known for just over a quarter of the species. Two chromosome numbers, $x = 7$ and $x = 8$, and three ploidy levels, $2n = 2x = 14$, $2n = 4x = 28$, $2n = 8x = 56$ and $2n = 2x = 16$, $2n = 4x = 32$, are present in the genus.

Studies on the impact of karyotypic characters on the interspecific and phylogenetic relationships and also on meiotic behaviour in the genus are still limited (Ranjbar et al., 2009b).

The evolutionary trend in *Onobrychis* has been discussed briefly based on the chromosome number. Goldblatt (1981) suggested that $x = 8$ is ancestral in the genus and those species with $x = 7$ are derived through aneuploid loss. However, Falistocco (1991) and Gomurgen (1996) argued that evolution within the genus has occurred by increasing the basic number from $x = 7$ to $x = 8$. Phylogenetic studies based on other lines of evidence have indicated that the primary centre of genetic diversity of *Onobrychis* is in the Mediterranean region and that the ecological

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separation of this region into western and eastern sectors represents a main event in the evolution of the genus (Ashurmetov and Normatov, 1998).

The present work aimed at increasing the knowledge about chromosome numbers and meiotic behaviour of the two Iranian populations of *O. chorassanica* belonging to the *O. sect. Hymenobrychis*. Such findings would help researchers to promote the understandings of the relationships between the chromosomal criteria and taxonomic delimitations.

Materials and methods

Chromosome number and meiotic behaviour were analyzed in two populations of *O. chorassanica*. These populations were collected from different regions of Khorasan Province; located between Quchan and Sabzevar (13636), and Mashhad and Chenaran, Ferazy village (13639). For cytogenetic study, 15 young flower buds from at least 5 plants at an appropriate stage of development were fixed in 96% ethanol, chloroform and propionic acid (6:3:2) for 24 h at room temperature and then stored in 70% alcohol at 4°C until used. Anthers were squashed and stained with 2% acetocarmine. All slides were made permanent by the Venetian turpentine. Photographs of chromosomes were taken on an Olympus BX-41 photomicroscope at initial magnification of X 1000. Chromosome counts were made from well-spread metaphases in intact cells, by direct observation and from photomicrographs. Voucher specimens are kept at BASU, Hamedan, Iran.

Results

All the studied samples from both populations were diploid and possessed $2n = 2x = 14$ chromosome number, consistent with the proposed base number of $x = 7$. Two populations of *O. chorassanica* were also investigated here for meiotic behaviour of their pollen mother cells (PMCs). Data with regard to the meiotic stage as well as abnormalities that observed in each stage is presented in table 1. A total of 1476 diakinesis/metaphase I (D/MI), 680 anaphase I/telophase I (AI/TI), 277 metaphase II (MII) and 470 anaphase II/telophase II (AII/MII) cells were analyzed. The meiotic irregularities observed in the studied taxa included: chromosome stickiness, B-chromosomes, precocious division of centromeres, chromosome bridges resulting from stickiness, the occurrence of laggard chromosomes, formation of micronuclei in tetrad cells, formation of tripolar

cells, desynapsis and cytomixis which have been discussed below (figure 1).

Discussion

Results showed that both populations were diploid and possessed $2n = 2x = 14$ chromosome number, consistent with the proposed base number of $x = 7$. Goldblatt (1981) suggested $x = 14$ as the basic number for the subfamily Faboideae, $x = 8$ for the tribe Hedysareae and $x = 8$ or 7 for the genus *Onobrychis*. He assumed that $x = 8$ is ancestral in the genus and that species with $x = 7$ are derived through aneuploid loss. The occurrence of the aneuploid series of $2n = 22, 27, 28$ and 29 in *O. viciifolia*, i.e. $2n = 3x + 1, 4x - 27, 28$ and 29 in *O. viciifolia*, i.e. $2n = 3x + 1, 4x - 1, 4x$ and $4x + 1$, respectively (Corti 1930; Sacristan 1966) demonstrates the role of aneuploid alteration from the higher chromosome numbers based on multiples of $x = 7$ in the evolution of the species. Then, we confirmed that the chromosome number of $x = 7$ in *O. sect. Hymenobrychis* has been derived from other numbers through aneuploid changes of the diploid or polyploid numbers.

Stebbins (1974) reported that the presence of more polyploid species than diploids in a genus is the evidence that these species have a geographical distribution different from those of their diploid ancestors. Ashurmetov and Normatov (1998) assumed that the primary centre of genetic diversity of the genus *Onobrychis* is the Mediterranean countries, while Yildiz et al., (1999) and Ranjbar et al., (2009b) argued that it is in north and-south western Asia. The observations of the present study as well as the available data on chromosome number of *Onobrychis* indicate that, among the approximately 50 species with known chromosome counts, the diploid species, either annual or perennial, represent 40% of the whole, while the polyploids represent 60%. Polyploids are encountered mainly in north-western Asia, especially in Anatolia, Turkey, Turkmenistan and Uzbekistan. Diploids are distributed throughout temperate Asia, Mediterranean countries and south-western Asia especially Iran.

Meiosis is an event of high evolutionary stability which culminates in a reduction of chromosome number. The normal and harmonious course of meiosis ensures gamete viability. The cytological events of gametogenesis are controlled by a large number of genes that act from premeiotic to postmeiotic mitosis. Mutations in these genes cause anomalies that may impair fertility. Furthermore, many abnormalities affecting plant fertility or

causing total male sterility have been detected during the evaluation of meiotic behaviour in some species.

Laggard, fragmented and sticky chromosomes

Laggards, for being unable to orient at the metaphase plate were observed during metaphase I.

The laggards at this phase of division might have been degenerated or may have resulted in the formation of polyads particularly at the resting phase (Basi et al., 2006). According to Nicklas and Ward (1994), non-oriented bivalents may be related to impaired attachment of kinetochores to the spindle fibers. Pagliarini (1990) reported that

Table 1. Number of pollen mother cells (PMCs) analyzed and percentage of PMCs meiotic behaviour in two population of *Onobrychis chorassanica*.

Populations	cho39 (Mashhad)	cho36 (Quchan)
Meiotic characters		
Total cell number	776	700
<u>D/MI</u>	51	86
% D/MI	6.57	12.2
% Cytoplasmic connection	11.76	0
% Sticky & laggard chromosome	5.88	19.76
% B-chromosome	0	2.32
% Precocious segregation	0	4.32
<u>AI/TI</u>	358	320
% AI/TI	46.13	45.5
% Fragmented chromosome	0.27	0
% Laggard chromosome	0.27	0
% Bridge	0.27	1.4
<u>MII</u>	157	120
% MII	20.23	17.4
% Fragmented chromosome	5.73	0
% Desynapsis	3.18	0
% Micronucleus	3.18	46.6
% Cytomixis	1.27	0
% Asynchronous nucleus	0	20
<u>AII/TII</u>	210	260
% AII/TII	27.06	14.45
% Micronucleus	0.47	0
% Tripolar cell	0.47	0
% Cytomixis	0	0.47
<i>N</i>	7	7

Abbreviations: D/MI = Diakinesis/Metaphase I; AI/TI = Anaphase I/Telophase I; MII = Metaphase II; AII/TII = Anaphase II/Telophase II; *n* = Chromosome number.

laggards may result from late chiasma terminalization. Ascending chromosomes are the result of precocious migration. According to Utsunomiya et al., (2002), they generally consist of univalent chromosomes formed during late prophase stages by precocious chiasma terminalization in early metaphase I. They may even result from low chiasma frequency or from the presence of asynaptic or desynaptic genes (Pagliarini, 2000). Laggards may produce micronuclei, if they fail to reach the poles in time to be included in the main telophase nucleus (Koduru

and Rao, 1981; Utsunomiya et al., 2002), leading to the formation of micro-pollen and probably to gametes with unbalanced chromosome numbers (Mansuelli et al., 1995), such as aneuploids (Defani-Scoarize et al., 1995). Laggards were observed in both populations.

B-chromosomes

B-chromosomes or accessory chromosomes that occur in addition to the standard or A-chromosomes in some plants, are smaller than other chromosomes and do not form any association with them. B-

chromosomes, when present in high numbers affect negatively the growth and vigor of the plants, while in low numbers may benefit the plant possessing them (Jones and Houben, 2003). B-chromosomes were observed only in Quchan population (figure 1H).

Precocious division of centromeres

In Quchan population, the number of cells with univalents presenting precocious migration to the poles during metaphase I was high (figure 1I),

while this abnormality was not observed in Mashhad population. Because univalents usually do not suffer regular segregation in the first division, the frequency of univalents in diakinesis/metaphase I, has been used as a standard measure of meiotic disturbances in other species (Scholes and Kaltsikes, 1974).

Cytomixis

The phenomenon of cytomixis consists in the migration of chromosomes between meiocytes

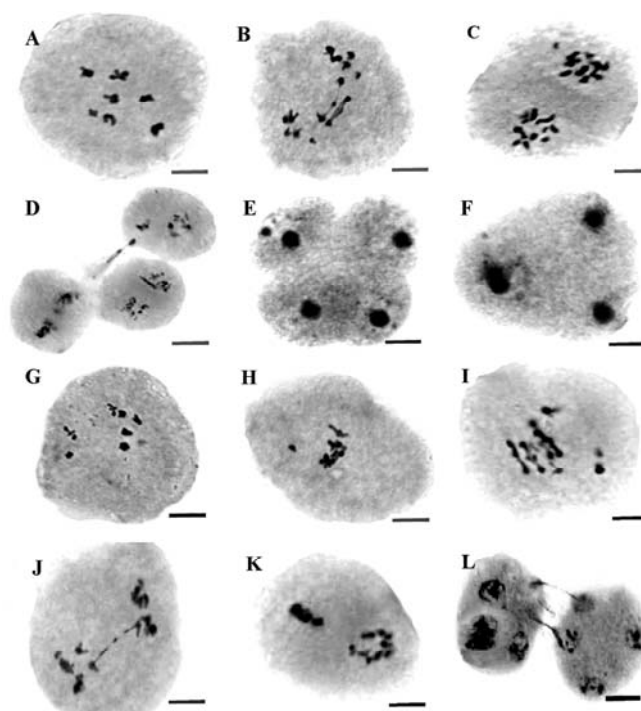


Figure 1. (A – F) Representative meiotic cells in Mashhad population of *O. chorassanica*: (A) Diakinesis. (B) Bridge. (C) Desynapsis. (D) Cytomixis. (E) Micronucleus. (F) Tripolar cell. (G – L) Representative meiotic cells in Quchan population of *O. chorassanica*: (G) Diakinesis. (H) B-chromosome. (I) Metaphase I with univalent in precocious ascension. (J) Bridge. (K) Asynchronous nucleus. (L) Cytomixis (Scale bar = 3 μ m).

through cytoplasmic connection. Since cytomixis creates variation in the chromosome number of the gametes, it could be considered as a mechanism of evolutionary significance (Ghaffari, 2006). This phenomenon was occurred in both populations in metaphase II and telophase II cells (figures 1D and L).

Chromosome bridges

Chromosome bridges resulting from stickiness were observed in two populations in anaphase I cells (figures 1B and J). The thickness of bridges observed and the number of chromosomes involved in their formation varied among different meiocytes. Genetic as well as environmental factors have been considered as the reasons for

chromosome stickiness in different plant species (Nirmala and Rao, 1996).

Micronucleus

Micronucleus is another abnormality that was found in both populations (figure 1E). Chromosomes that produced micronuclei during meiosis were eliminated from microspores as microcytes. The micronucleus reached the microspore wall and formed a kind of bud, separated from the microspore. The eliminated microcytes gave origin to small and sterile pollen grains (Baptists-Giacomoelli et al., 2000).

Tripolar cells

Failure of chromosome movement occurred in

one of the poles of anaphase cells, leading to the formation of tripolar cells. Such cells produce normal reduced and unreduced daughter cells. This phenomenon was found in Mashhad population (figure 1F). Such unreduced meiocytes may lead to the information of $2n$ pollen grains (Sheidai et al., 2007).

In conclusion, both diploid populations of *O. chorassanica* with the chromosome basic number of $2n = 2x = 14$ showed different meiotic abnormalities. These abnormalities were observed in Mashhad population in higher frequencies than those in Quchan. They are genetically controlled and have been reported in populations of different legume species like *Oxytropis* and *Astragalus*

(Ranjbar et al., 2010a, b). Varied ranges of meiotic abnormalities in populations with the same chromosome number is considered as a means for generating different kinds of recombinants, influencing the variability within natural populations in a possibly adaptive manner (Rees and Dale, 1974). Like other meiotic abnormalities, cytomixis occurred in Mashhad population higher than in Quchan. Cytomixis may lead to production of aneuploid plants or result in the production of unreduced gametes, as reported in several species. Unreduced gamete formation is of evolutionary importance as it can lead to the production of plants with higher ploidy level (Falistocco et al., 1995).

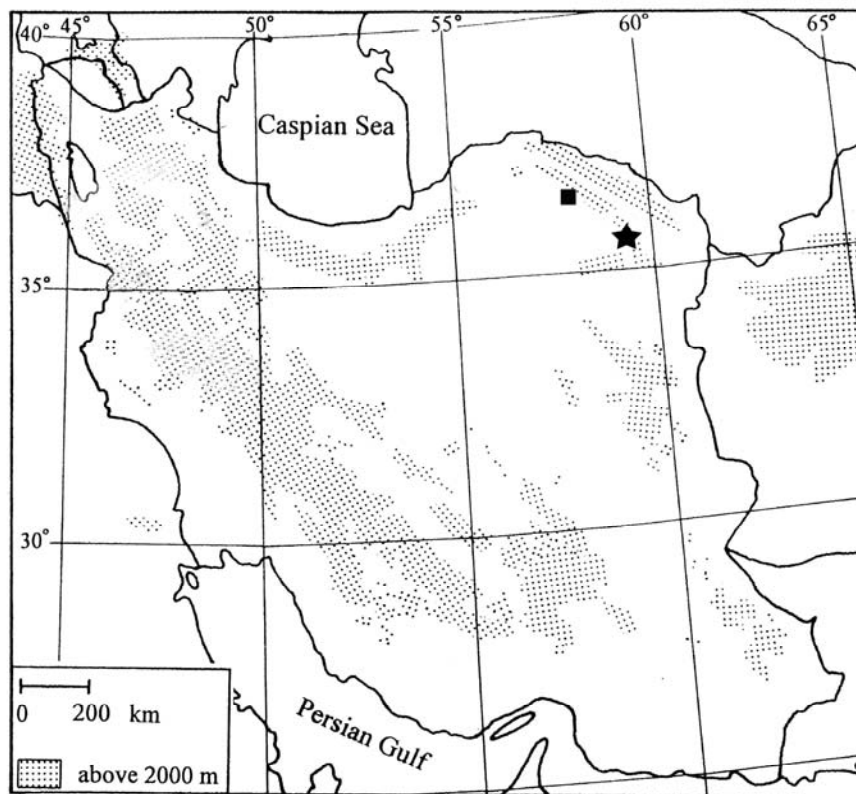


Figure 2. Distribution of Mashhad (★) and Quchan (■) populations of *Onobrychis chorassanica* in Khorassan Province.

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