

REVIEW

Chromosome evolution in marginal populations of *Aegilops speltoides*: causes and consequences

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• **Background** Genome restructuring is an ongoing process in natural plant populations. The influence of environmental changes on the genome is crucial, especially during periods of extreme climatic fluctuations. Interactions between the environment and the organism manifest to the greatest extent at the limits of the species' ecological niche. Thus, marginal populations are expected to exhibit lower genetic diversity and higher genetic differentiation than central populations, and some models assume that marginal populations play an important role in the maintenance and generation of biological diversity.

• **Scope** In this review, long-term data on the cytogenetic characteristics of diploid *Aegilops speltoides* Tauch populations are summarized and discussed. This species is distributed in and around the Fertile Crescent and is proposed to be the wild progenitor of a number of diploid and polyploid wheat species. In marginal populations of *Ae. speltoides*, numerical chromosomal aberrations, spontaneous aneuploidy, B-chromosomes, rDNA cluster repatterning and reduction in the species-specific and tribe-specific tandem repeats have been detected. Significant changes were observed and occurred in parallel with changes in plant morphology and physiology.

• **Conclusions** Considerable genomic variation at the chromosomal level was found in the marginal populations of *Ae. speltoides*. It is likely that a specific combination of gene mutations and chromosomal repatterning has produced the evolutionary trend in each specific case, i.e. for a particular species or group of related species in a given period of time and in a certain habitat. The appearance of a new chromosomal pattern is considered an important factor in promoting the emergence of interbreeding barriers.

Key words: *Aegilops speltoides*, wheat, marginal populations, chromosomes, evolution, speciation.

INTRODUCTION

The influence of environmental changes on the genome is crucial, especially during periods of extreme climatic fluctuations. It is generally accepted that plant genomes respond to variations in environmental conditions and that the large-scale features of plant systems (such as yield and sustainability) depend on interactions between individual plants and environmental factors (Yin and Struik, 2007; Martienssen, 2008). Interactions between the environment and the organism manifest to the greatest extent at the limits of the species' ecological niche. The central–marginal hypothesis states that two key genetic parameters – the effective population size and the rate of gene flow – should be highest at the range centre and lowest at the range margins (for a review, see Eckert *et al.*, 2008). Thus, marginal populations are expected to exhibit lower genetic diversity and higher genetic differentiation than central populations. At the same time, in marginal populations under the influence of an unusual ecology, intensive processes of riation and speciation may take place, and some models assume that marginal populations play an important role in the maintenance and generation of biological diversity (Mayr, 1970; Kirkpatrick and Barton, 1997; Grant, 1981; Channell and Lomolino, 2000; Navarro and Barton, 2003). Indeed, the genomic changes in marginal populations that experience strong selective forces could be key for

understanding genomic evolution and for predicting the response of a genome to environmental changes.

Here, I summarize our long-term data on the cytogenetic characteristics of natural populations of diploid *Aegilops speltoides* Tausch ($2n = 2x = 14$) with special emphasis on small, marginal, stressed populations. This species belong to sect. *Sitopsis* (Triticeae, Poaceae), is distributed in and around the Fertile Crescent and is proposed to be the wild progenitor of a number of diploid and polyploid wheat species (Sears, 1941; Zohary and Imber, 1963; Kimber and Feldman, 1987). Currently in the Middle East region, we observe recession of a plant range to the north (Tchernov, 1988; Hofreiter and Stewart, 2009; <http://www.ipcc.ch>) which is a common event when climate changes. This scenario repeatedly occurred during the glacial period and the subsequent Holocene. This is a unique opportunity to observe the reaction of the genome of a model group of species to a changing environment, as Middle Eastern flora might be the first to experience the impact of global warming due to the close proximity to the African–Arabian desert domain. Comparative cytogenetic study of genome evolution in natural plant populations throughout the species' range yields a snapshot of the genome state, and if the cytogenetic findings are combined with data from the fields of molecular genetics and botany, they may shed light on past, current and even future evolutionary events.

MARGINAL POPULATIONS: A SOURCE OF A NEW FORMS AND SPECIES

Defining marginal populations

The importance of clearly defining marginality should be emphasized. The main criteria we used for assigning populations of *Ae. speltoides* to the marginal category were as follows: (1) the position relative to the centre of the species' range; (2) the population size (the area of small populations is $<1000\text{ m}^2$); (3) the degree of population destruction (mainly due to human activity); (4) local ecology (biotic and abiotic components); and (5) elevation (the optimum is from 100 to 1000 m asl). The current centre of the *Ae. speltoides* range is in the middle of the Fertile Crescent (Zohary *et al.*, 1969; Zohary, 1970; Kimber and Feldman, 1987) and is limited to the approximate geographic coordinates $36\text{--}38^\circ\text{N}$, $37\text{--}41^\circ\text{E}$ (a list of the investigated populations and their characteristics is shown in the Appendix). All Israeli populations of *Ae. speltoides* are peripheral and located at the southern border. The northernmost populations in Turkey could also be regarded as peripheral. Among the ten investigated Israeli populations (Raskina *et al.*, 2011), only two fell under the definition of marginal, specifically a population near the mouth of the Kishon River (Kishon population) and the populations on the northern slope of Carmel Mountain which no longer exist (Technion 2 population). Both populations are extremely small (approx. 100 m^2 and 20 m^2 , respectively). The Kishon population is the only Israeli population that is located at sea level (2 m asl) and is close to the Akko plain terminal of desert plants (Raskina *et al.*, 2004a, b, 2011). Technion 2 and the neighbouring population, Technion 1, represent the remnants of a once large single population; we have observed the continuing, rapid decline of this population over the last decade. Despite the negative impact of anthropogenic factors, the main factor in the rapid decline of the remnants of the original Technion population is climate change, which has led to the displacement of local flora by other species.

The northernmost Turkey populations (Appendix) also fall under the definition of marginal.

Morphological and physiological characteristics of plants from peripheral and marginal populations

In marginal populations, changes in plant morphology and physiology have been observed. In the case of the marginal population of *Ae. speltoides* from Cankiri (Turkey), adult plants grown in a greenhouse were half the size of phenotypically normal plants and had smaller spikes of 3.5–4.5 cm. The time from germination to flowering was up to a year, which is longer than the typical 6–7 months (Appendix). It should be noted that this was the northernmost population of all of those investigated, and the winter-type characteristic of the population explains the delay in development in the absence of vernalization. The exact opposite was observed for the southernmost Kishon population. The time from germination to flowering was found to occur in half the expected time, a maximum of 3–3.5 months. Interestingly, despite the short vegetative phase, the maturation of the seeds in this population occurred only 10–14 d earlier than in the neighbouring populations on Mount Carmel, which exhibit a normal life cycle (Technion, Nahal Mearot and Ramat Hanadiv) (Appendix).

Another important feature of the species is spike morphology. *Aegilops speltoides* has a unique genetic dimorphism in the fruit types (Fig. 1A). Both morphotypes, dominant *ligustica* and recessive *aucheri*, are encoded by tightly linked genes (Sears, 1941; Zohary and Imber, 1963; Kimber and Feldman, 1987). In nature, both subspecies coexist in mixed cross-pollinated populations. The ratio of the *ligustica*–*aucheri* morphotypes varies significantly between populations and very probably depends on environmental conditions. Over the past 12 years, we recorded a large shift in the Kishon population towards the *ligustica* phenotype; however, in the small Technion 1 population, the last few plants with the *ligustica*

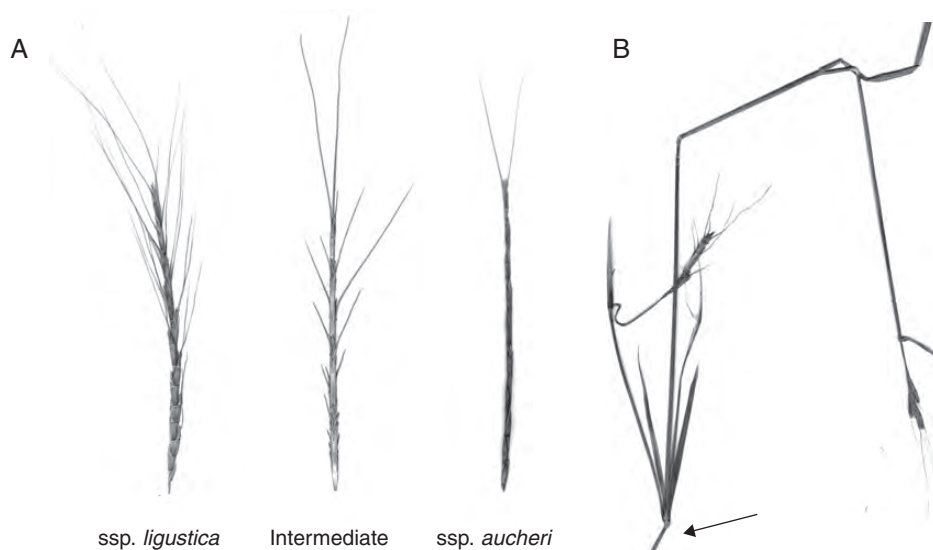


FIG. 1. Morphological characteristics of *Ae. speltoides*. (A) Left, normal spike from *Ae. speltoides* ssp. *ligustica*; right, normal spike from *Ae. speltoides* ssp. *aucheri*; centre, abnormal intermediate phenotype. (B) The atypical development of a secondary tiller from the lateral bud (arrowed) on the main culm.

morphotype were observed in 2002, and this small population has become homogeneous and currently consists of only plants with the *aucheri* phenotype. In the last decade, these two populations diverged considerably. I recently discovered a similar small population consisting only of the *aucheri* morphotype at the foot of the Carmel Mountain in the Nahal Mearot Valley and an En-Efek population in the Akko coastal plain consisting only of the *ligustica* morphotype (Appendix), which suggests that this phenomenon is not unique. Another morphological alteration was found in populations of Ramat Hanadiv and Givat Koah (Fig. 1A). It is expressed in an intermediate abnormal *ligustica*–*aucheri* phenotype, and may be caused by genetic changes within the linked group of genes. These plants have spikes that resemble the *aucheri* type (i.e. not brittle) but also have pronounced lateral awns similar to the *ligustica* type. A large number of plants collected in various remote locations from the main population of Ramat Hanadiv indicate that this seemingly neutral mutation has already become fixed in the population. In addition to this abnormality, we also noted the development of secondary tillers from the lateral buds of the main culm and even tertiary tillers, which is atypical for *Ae. speltoides* (Fig. 1B). The same anomaly was also documented in plants from the Cankiri population (Turkey). Evidently, the identified population-specific alterations in the life cycle and phenotype of *Ae. speltoides* are caused by as yet unknown gene mutations and/or chromosomal rearrangements, which result in changes in gene arrangement and/or gene expression.

Chromosomal rearrangements and genomic repatterning in *Ae. speltoides*

Natural populations are known to be enriched with chromosomal rearrangements that generally occur in the heterozygous state (White, 1978; Rieseberg, 2001; Levin, 2002). The effect of chromosomal rearrangements is suppression of recombination within rearranged regions (inversions), the disruption of existing linkage groups and the creation of new ones (translocations), which may lead to changes in gene expression and in the interactions between genes (Rieseberg, 2001; Strasburg *et al.*, 2009; Brown and O'Neill, 2010). Some chromosomal rearrangements may be neutral without significant effect on the phenotype. Nevertheless, underlying heteromorphism in homologous chromosomes may create intraspecific polymorphisms in the heterochromatin pattern. In contrast, it is thought that the majority of chromosomal rearrangements that involve euchromatin are deleterious and can be maintained in a population only in the heterozygous state because the homozygote is eliminated by natural selection (Levin, 2002; Charlesworth, 2009; Brown and O'Neill, 2010; Faria and Navarro, 2010). However, some chromosomal aberrations may become fixed in the population by positive selection if they are associated with the emergence of an adaptive combination of traits, especially in a changing environment (Kirkpatrick and Barton, 1997; Hoffmann *et al.*, 2004; Coghlan *et al.*, 2005; Orr, 2005; Kirkpatrick and Barton, 2006; Rieseberg and Willis, 2007; Charlesworth, 2009). The frequency and spectrum of chromosomal repatterning, which are determined by external (biotic and abiotic) and internal

(such as population size and mating system) factors, are indicators of the population's state in time and space.

Numerical chromosomal aberrations in Ae. speltoides populations: spontaneous aneuploidy and B-chromosomes. Spontaneous aneuploidy is not a normal and stable state of the diploid genome. Additional chromosomes resulting from meiotic disruption further destabilize the genome through the disruption of normal chromosome pairing and segregation. The result may be lethal or at least cause a decrease in fertility. In populations of *Ae. speltoides*, aneuploidy may occur for individual chromosomes as a result of gene mutations or/and meiotic disorders, but spontaneous non-disjunction of the entire chromosome complement can also occur. The triploid genotype found in the Ramat Hanadiv population is an example of the latter and is shown in Fig. 2A; curiously, an additional B-chromosome is also present. The emergence of supernumerary B-chromosomes (Bs) is another consequence of genomic aberrations in natural *Ae. speltoides* populations (Fig. 2B). The presence of Bs, similar to aneuploidy, increases the frequency of recombination, thereby causing new chromosomal abnormalities (Mendelson and Zohary, 1972; Zarchi *et al.*, 1974; Cebria *et al.*, 1994; Camacho *et al.*, 2000, 2002; Puertas, 2002; Jones and Houben, 2003; Jones *et al.*, 2008a, b; Belyayev *et al.*, 2010). We detected up to eight Bs in natural populations of *Ae. speltoides* (Raskina *et al.*, 2011). Interestingly, the presence of from one to three Bs has a positive effect on the plant, whereas a higher number of Bs reduces fertility and vigour (Mendelson and Zohary, 1972; Belyayev *et al.*, 2010). If there are only two Bs in a genome, they often behave like normal homologues in meiosis by forming a bivalent and then separating normally to opposite poles during anaphase I. However, increases in the number of Bs further destabilize the genome by promoting heterologous recombination and meiotic aberrations. The ability for heterologous conjugation with the A-chromosomes is due to the structural organization of Bs in *Ae. speltoides*. A well-known and important feature of Bs in plants and animals is a high proportion of heterochromatin, which is gained through the accumulation of different types of repetitive DNAs, including transposable elements (Puertas, 2002; Jones and Houben, 2003; Jones *et al.*, 2008a, b; Carchilan *et al.*, 2009). In *Ae. speltoides*, all Bs carry a single intercalary *Spelt 1* tandem repeat cluster and a 5S rDNA cluster in both arms (Figs 2A, B and 3A, B) (Raskina *et al.*, 2011). In addition, as shown in Fig. 2B, a large intercalary cluster of Ty3-gypsy elements was found in close proximity to the 5S rDNA and *Spelt 1* blocks. Clusters of highly repetitive DNA such as 5S rDNA, tandem repeats, clusters of transposable elements, and telomere and centromeric repeats are the hot spots for homo- and heterologous synapses and recombination between chromosomes of the types A–A and A–B in meiosis. An example of synapses between Bs and A-chromosomes is shown in Fig. 3A, B. The similarity in the B-chromosome structures throughout the species range caused us to hypothesize that they were generated from similar processes, specifically the heterologous recombination of certain A-chromosomes. We suggest that chromosome 4, which only carries the intercalary *Spelt 1* cluster, and chromosome 5, which is an exclusive source of 5S rDNA in the genome of *Ae. speltoides*, may be involved in the heterologous synapses and recombination resulting in the formation of Bs (Raskina *et al.*,

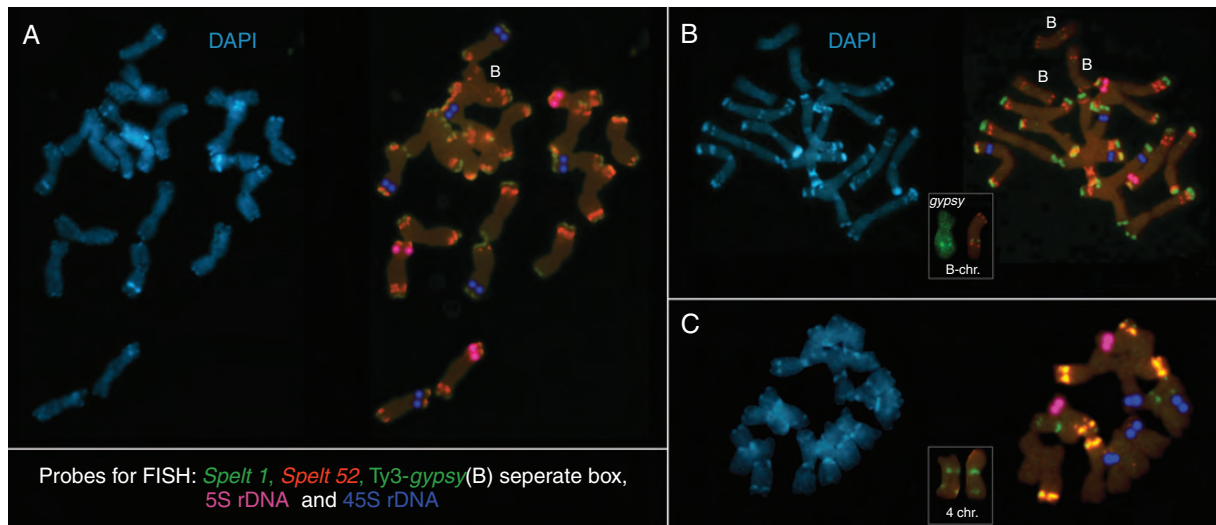


FIG. 2. Fluorescence *in situ* hybridization (FISH) on somatic chromosomes of *Ae. speltoides* with *Spelt 1* (green), *Spelt 52* (red), As5SDNAE (5S rDNA, pink pseudocolour) and pTa71 (45S rDNA, blue pseudocolour) DNA probes, and differential staining with 4',6-diamidino-2-phenylindole (DAPI). (A) Original triploid genotype from the Ramat Hanadiv population; one B-chromosome also appears. (B) Diploid genotype with three Bs from the Ramat Hanadiv population. Inset B-chromosomes: left, large intercalary Ty3-gypsy cluster (Belyayev *et al.*, 2001) in the long arm; right, intercalary *Spelt 1* and 5S rDNA clusters in the long arm and a distal 5S rDNA cluster in the short arm. (C) Metaphase plate of the plant from the marginal Cankiri population: loss of almost all terminal *Spelt 1* and a reduced number of *Spelt 52* clusters in comparison with the Ramat Hanadiv population. Inset: chromosome 4 contains intercalary and near-centromeric *Spelt 1* clusters.

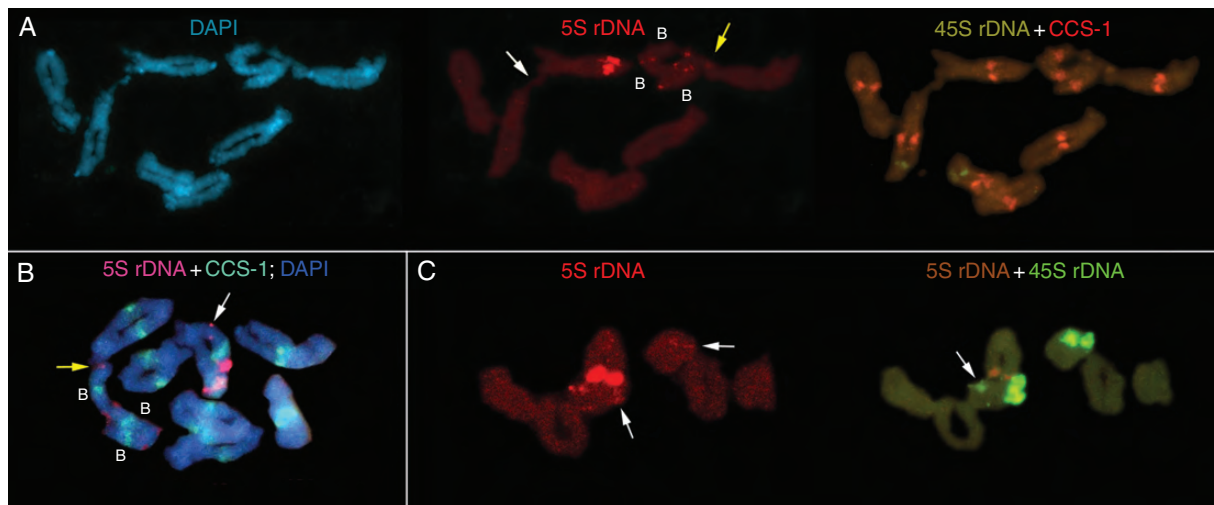


FIG. 3. Fluorescence *in situ* hybridization (FISH) on meiotic chromosomes of *Ae. speltoides* from the Kishon population with As5SDNAE (5S rDNA, red), pTa71 (45S rDNA, green), CCS-1 [cereal centromere sequence, green (Aragon-Alcaide *et al.*, 1996)]. (A) Heterologous synapses between the long arms of chromosomes 5 and 1 (white arrow) and between B- and A-chromosomes (yellow arrow). (B) A synapse between A- and B-chromosomes is shown with a yellow arrow; chromosome 5 is heterozygous for pericentric inversion and carries an intercalary additional 5S rDNA cluster (white arrow). (C) Left, two additional 5S rDNA clusters are marked with arrows; right, a cell-specific additional 45S rDNA intercalary cluster is marked with an arrow.

2011). The emergence of Bs in the population usually accompanies outcrossing; however, an important feature of *Ae. speltoides* is that it is highly self-compatible and reproduces effectively in both cross- and self-pollination mating systems (Zohary and Imber, 1963; Raskina *et al.*, 2004b; Belyayev *et al.*, 2010). It is very likely that the dualism of their reproduction system in combination with dimorphism (the coexistence of the *aucheri* and *ligustica* morphotypes in natural panmictic populations) is the basis for the evolutionary lability of the *Ae. speltoides* genome, determines its direct involvement in

the generation of allopolyploid wheats and probably allowed it to become a progenitor for the sect. *Sitopsis* (Raskina *et al.*, 2004b).

Structural chromosome aberrations: reduction in the species-specific Spelt 1 and tribe-specific Spelt 52 tandem repeats in peripheral and marginal populations of Ae. speltoides. Significant intraspecific polymorphisms in the distribution of *Spelt 1* and *Spelt 52* tandem repeats that are integral parts of heterochromatin were found in *Ae. speltoides* (Raskina *et al.*, 2011). The

heterochromatin chromosomal pattern is one of the most important characteristics of a species. Nevertheless, there is a significantly high level of intraspecific C-banding polymorphisms in the *Aegilops/Triticum* complex (Friebe and Gill, 1996; Maestra and Naranjo, 1999; Maestra and Naranjo, 2000; Badaeva *et al.*, 2002, 2004, 2007). In the 1970s, research on the inheritance of Giemsa C-bands showed Mendelian segregation in successive generations under self-pollination, which provided direct evidence that meiotic crossing-over caused the variation in the heterochromatic patterning of rye (Singh, 1977), barley (Linde-Laursen, 1979) and maize (Handlaczky and Kalman, 1975). Tandem repeats comprise a significant portion of the distal and terminal heterochromatin of the *Aegilops* and *Triticum* genomes (Anamthawat-Jonsson and Heslop-Harrison, 1993; Salina *et al.*, 2006; Zoshchuk *et al.*, 2007). The intraspecific chromosome patterns of the species-specific *Spelt 1* and tribe-specific *Spelt 52* tandem repeats in *Ae. speltoides* are highly variable. We observed an almost complete loss of the terminal *Spelt 1* repeats in marginal populations (Fig. 2C), in which the number of blocks was 12–14 times lower than in central populations (Raskina *et al.*, 2011). The number of *Spelt 52* blocks was also 1.5–2 times lower in intermediate and marginal populations than in central populations (Fig. 2B). Intraspecific polymorphisms of the *Spelt 1* and *Spelt 52* tandem repeat chromosomal patterns are a special case of heterochromatin pattern polymorphism and a result of complex chromosomal rearrangements in the panmictic populations of outcrossing *Ae. speltoides*, as these polymorphisms reflect random chromosomal recombination under random mating (Raskina *et al.*, 2004a; Belyayev *et al.*, 2010). The number of *Spelt 52* clusters in successive generations under self-pollination follows chromosomal segregation, while the copy number abundance of this tandem repeat in each successive genome is subject to amplification or reduction as a consequence of homologous and/or heterologous recombination in distal/terminal chromosomal regions. We propose that the depletion of tandem repeats in the marginal populations of *Ae. speltoides* could be a result of either elimination of the repeats under stressful environmental conditions in the peripheral populations or amplification of the repeats in conducive climatic and/or edaphic environments in the centre of the species' geographical distribution. It is likely that both scenarios have occurred simultaneously and that we observed a bidirectional shift in the repetitive DNA genomic patterns that led to interpopulation diversification. In the central populations with optimal environmental conditions, the current chromosomal rearrangements, such as duplications and insertions caused by unequal crossing-over and/or reciprocal balanced translocations, contribute to the accumulation of tandem repeats in the population. In peripheral and marginal populations, an increase in the recombination frequency under stressful conditions (Grant, 1981; Levin, 2002; Belyayev *et al.*, 2010; Raskina *et al.*, 2011) leads to unbalanced translocations and multiple deletions that involve more breakpoints, which dominate over other types of structural chromosomal mutations. Consequently, we witnessed the loss of a large number of *Spelt 1* and *Spelt 52* clusters. The appearance of a new chromosomal pattern is considered an important factor in the diversification of populations and the prevention of cross-breeding.

Among structural chromosomal rearrangements, inversions are especially important for the creation of interbreeding barriers. In the genome of *Ae. speltoides*, the intercalary position of *Spelt 1* cluster(s) indicates the probable presence of an inversion(s) in chromosome 4 (Raskina *et al.*, 2011) (Fig. 2C inset). An important feature of inversions is that they appear to be a source of particular adaptive combinations of genes (Grant, 1981; Rieseberg and Willis, 2007), and could capture and spread locally adapted alleles in a population by suppressing recombination between the loci (Hoffmann *et al.*, 2004; Kirkpatrick and Barton, 2006). Survival and reproduction of self-compatible genotypes may give rise to an endemic form of the species that is adapted to the new environment, while the parental species recedes or disappears (Lewis and Raven, 1958; Lewis, 1962; Grant, 1981; Tchernov, 1988). We propose that the scenario of sympatric speciation has occurred in the sect. *Sitopsis* in the periphery of the *Ae. speltoides* range subjected to a changing environment (Raskina *et al.*, 2004b).

Rearrangements of ribosomal DNA sites. In addition to the major chromosomal rearrangements that I described above, it is also possible to estimate the level of microevolutionary genomic change indirectly by evaluating the repatterning of well-defined chromosomal markers and, primarily, by the mobility of rDNA clusters. Both the location and number of rDNA sites vary intraspecifically (Eickbush and Eickbush, 2007). The variation may involve major loci, or fragments of the unit (Fig. 3C), and these are often not known to be transcribed (Heslop-Harrison, 2000). The mechanism for rDNA cluster repatterning could be unequal crossing-over (Eickbush and Eickbush, 2007) or the activity of adjacent transposable elements (Raskina *et al.*, 2004a, b, 2008). It is obvious that chromosomal repatterning further increases/decreases the number of rDNA sites or their repositioning, but the dynamics of rDNA clusters may be regarded as a strong indicator for ongoing significant microevolutionary processes (Jiang and Gill, 1994; Raskina *et al.*, 2004b).

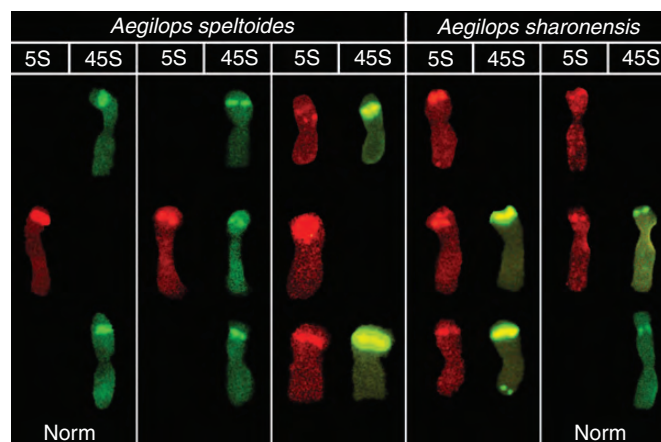


FIG. 4. Chromosomal pattern of 5S rDNA (red) and 45S rDNA (green) of *Ae. speltoides* and *Ae. sharonensis* from the Kishon populations (Raskina *et al.*, 2004b). Modified genotypes of both species carry additional rDNA clusters on the chromosomes 1, 5 and 6.

In the marginal Kishon population, we discovered modified genotypes of *Ae. speltoides* with rDNA patterns similar to those of the closely related species *Ae. sharonensis*. Likewise, *Ae. sharonensis* plants from the bordering population in the Kishon area possessed *Ae. speltoides*-like features, including additional 5S and 45S ribosomal sites in both species on chromosomes 1, 5 and 6, which differed from the usual rDNA patterning for this species (Fig. 4). We speculate that the increased ratio of self-pollination and inbreeding in a stressful environment induced rDNA repatterning in this small marginal population of *Ae. speltoides* (Raskina *et al.*, 2004b). We found further evidence to support this hypothesis. In the third successive generation of self-pollinated plants of *Ae. speltoides*, we found the *de novo* appearance of additional 5S rDNA clusters in regions of secondary constriction in chromosomes 1 and 6, but the maternal plant had normal rDNA patterning (Belyayev *et al.*, 2010). The process of rDNA repatterning is permanent in the Kishon population, and the emerging variants in most cases resemble the chromosomal rDNA pattern found in closely related species of the *Sitopsis* group. Thus, we propose that canalized repatterning of rDNA sites may eventually lead to sympatric speciation in marginal populations of *Ae. speltoides* (Raskina *et al.*, 2004b).

CONCLUDING REMARKS

In combination with gene mutations, the role of chromosomal rearrangements in the evolution of the eukaryotic genome has been debated for a long time (Dobzhansky, 1935; Mayr, 1970; White, 1978; Grant, 1981; Rieseberg and Willis, 2007; Brown and O'Neill, 2010). It is likely that a specific combination of gene mutations and chromosomal repatterning has produced the evolutionary trend in each specific case, i.e. for a particular species or group of related species in a given period of time and in a certain habitat (Dobzhansky, 1935). Changes in genomic structure are an ongoing process that occurs in natural populations. I have no uncontested evidence that there is a direct link between chromosomal rebuilding and changes in plant morphology and physiology, but I can at least say that these changes occur simultaneously. I propose that chromosomal repatterning in these cases might play a role in the development of new traits by breaking apart linkage groups, altering the interaction between genes and/or affecting gene expression.

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APPENDIX

Characteristics of the *Ae. speltoides* populations studied.

Populations, origin, source	Geographical zone, elevation, coordinates	Population size; location	Morphotype
Kirklareli, Turkey*, PI 170203	Euro-Siberian, 64 m, 41°20'N, 27°29'E	N/A; cultivated field [¶]	ssp. <i>ligustica</i>
Cankiri, Turkey†, PI 573448	Euro-Siberian, 680 m, 40°31'N, 33°38'E	N/A; cultivated field [¶]	ssp. <i>ligustica</i>
Ankara, Turkey*, PI 573452	Irano-Turanian, 575 m, 36°59'N, 32°56'E	N/A; cultivated field [¶]	ssp. <i>ligustica</i>
Eregli, Turkey‡, TS-24, G-1038	Irano-Turanian, 1200 m, 37°25'N, 34°15'E [¶]	N/A; natural habitat [¶]	ssp. <i>ligustica</i>
Gaziantep, Turkey†, TR 50279	Mediterranean, 940 m, 37°05'N, 37°24'E [¶]	N/A; urbanistic area [¶]	ssp. <i>aucheri</i>
Urfa, Turkey*, PI 542262	Mediterranean, 700 m, 37°17'N, 38°46'E	N/A; cultivated field [¶]	ssp. <i>ligustica</i>
Arbil, Iraq*, PI 219867	Irano-Turanian, 570 m, 36°24'N, 44°08'E	N/A; uncultivated area [¶]	ssp. <i>ligustica</i>
Latakia, Syria [§] , PI 487235, TS-84	Mediterranean, 200 m, 35°38'N, 35°59'E	N/A; uncultivated area [¶]	ssp. <i>aucheri</i>
Tartus, Syria*, PI 487238	Mediterranean, 600 m, 35°07'N, 36°07'E	N/A; cultivated field [¶]	ssp. <i>aucheri</i>
Achihood, Israel [§] , 2-16	Mediterranean, 45–75 m, 32°55'N, 35°10'E	Large; cultivated field and natural habitat	ssp. <i>ligustica</i> , ssp. <i>aucheri</i>
En-Efek, Israel [§] , 2-37	Mediterranean, 16 m, 32°50'N, 35°06'E	Small; uncultivated area; endangered	ssp. <i>ligustica</i>
Kishon, Israel [§] , 2-22	Mediterranean, 2 m, 32°48'N, 35°02'E	Small; natural habitat; endangered	ssp. <i>ligustica</i> , ssp. <i>aucheri</i> ,
Technion-1, Israel [§] , 2-36	Mediterranean, 224 m, 32°46'N, 35°00'E	Small; urbanistic area; endangered	ssp. <i>aucheri</i>
Technion-2, Israel [§] , 2-36	Mediterranean, 265 m, 32°46'N, 35°00'E	Small; natural habitat; extinct	ssp. <i>ligustica</i> , ssp. <i>aucheri</i>
Nahal Mearot, Israel [§] , 2-48	Mediterranean, 52 m, 32°40'N, 34°58'E	Small; natural habitat	ssp. <i>aucheri</i>
Ramat Hanadiv, Israel [§] , 2-46	Mediterranean, 100–125 m, 32°33'N, 34°56'E	Large; natural habitat; interrupted area	ssp. <i>ligustica</i> , ssp. <i>aucheri</i> , intermediate
Katzir, Israel [§] , TS 89	Mediterranean, 233–250 m, 32°29'N, 35°05'E	Large; natural habitat	ssp. <i>aucheri</i>
Givat Koah, Israel [§] , TS 43	Mediterranean, 75 m, 32°02'N, 34°58'E [¶]	Small; uncultivated area; extinct	Intermediate
Ashdod, Israel [§] , TS 93	Mediterranean, 35 m, 31°51'N, 34°45'E [¶]	N/A; uncultivated area; extinct	ssp. <i>ligustica</i>
Ashkelon, Israel [§] , TS 01	Mediterranean, 45 m, 31°40'N, 34°38'E [¶]	N/A; uncultivated area; extinct	ssp. <i>aucheri</i>

N/A, not available.

Source: *USDA, United States Department of Agriculture; †AARI, Aegean Agricultural Research Institute, Turkey; ‡kindly provided by Professor M. Feldman, Weizmann Institute collection, Rehovot, Israel; § IE, Institute of Evolution collection, Haifa, Israel.

[¶] Data obtained from Google Earth.