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Chromosome translocations in wild populations of tetraploid emmer wheat in Israel and Turkey

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Abstract Translocation frequencies (as compared to the standard chromosome arrangement typified by that in 'Chinese Spring') in 9 or more genotypes from each of 15 populations of *Triticum dicoccoides* in Israel were determined. Data also were obtained from 2 genotypes of the southernmost population (Jaba). A single population from Turkey was also investigated. There were 119 genotypes with translocations in the sample of 171 genotypes investigated (70%). The frequency of translocations in different populations varied from 0.27 to 1.00, and all populations had 1 or more genotypes with one or more translocations. Some populations such as Qazrin appeared to be homogeneous for translocations, but most populations were heterogeneous. A sample of 17 genotypes from 12 of the populations were crossed with the Langdon D-genome disomic substitutions to determine the identity of the chromosomes involved in the translocations. There were nine genotypes with translocations and with the exception of a 2A/2B translocation, none of them involved the same chromosomes. The B-genome chromosomes were involved in translocations more frequently than the A-genome chromosomes. Translocation frequencies (TF) of the various populations were correlated with environmental variables, primarily with water availability and humidity, and possibly also with soil type. In general, TF was higher in peripheral populations in the ecologically heterogeneous frontiers of species distribution than in the central populations located in the catchment area of the upper Jordan valley.

Key words *Triticum dicoccoides* · Translocation frequency · Chromosome pairing · Geography · Climate · Environmental association of translocations

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Introduction

'Chinese Spring' wheat (*Triticum aestivum* L.) has the standard chromosome arrangement, and most accessions of cultivated wheats, both tetraploid (*Triticum turgidum* L. var '*durum*') and hexaploid, have that arrangement. Therefore, the chromosomes at metaphase I (MI) of meiosis are arranged into 14 bivalent pairs in tetraploid species, into 21 bivalent pairs in hexaploids, with multivalents being rare.

Wild emmer wheat (*Triticum dicoccoides* Koern.), the wild tetraploid species from the Middle East, is probably a direct ancestor of all cultivated tetraploid and hexaploid wheats. Consequently, most accessions of this subspecies should have the standard chromosome arrangement. However, a translocation has been observed in a cross between a genotype of *dicoccoides* and 'Langdon' (LDN) durum wheat (Joppa and Cantrell 1990). Previously, Kawahara (1987) intercrossed a number of *dicoccoides* accessions and identified six different reciprocal translocations (Kawahara 1987).

Nishikawa et al. (1986) crossed a durum wheat line (Ld-221) that has the standard chromosome arrangement with other subspecific varieties of tetraploid wheat. *Ethiopicum* had a reciprocal translocation between 2A and 4A; the *Abyssinicum* type had two translocations that involved 4A/2A and 2A/2B; and *Liuguliforme* had two different translocations, one was 7A/5B, and the other was unidentified.

The occurrence of translocations in durum wheat bred in or introduced into Spain was investigated by Perera et al. (1983). They reported that 21 of 48 cultivars had a translocation (43.7%), but no attempt was made to determine if the translocations were the same or different, and many of the reported translocations involved related cultivars. The

true frequency of translocations in durum wheat lines and cultivars is unknown because they have not been extensively investigated in this subspecies.

T. dicoccoides found in wild populations in Israel and in Turkey have been extensively studied by Nevo and others (See Nevo and Beiles 1989 for a partial list of publications). Preliminary studies have indicated that reciprocal translocations in these populations are common (Kawahara et al. 1993). Therefore, the objectives of this study were: (1) to characterize a sample of genotypes from these populations across the species range in Israel for the frequency and diversity of reciprocal translocations, (2) to relate the occurrence of translocations to other previously studied characteristics of the populations, and (3) to attempt to gain a better understanding of their ecogeographical correlates and their evolutionary significance.

Materials and methods

Nevo and Beiles (1989) list 37 populations of *dicoccoides* (33 from Israel and 4 from Turkey). Their geographical distribution and their ecogeographical description is given in Fig. 1 and Table 1 of Nevo and Beiles (1989). From these populations, a sample of at least 9 genotypes (with the exception of only 2 genotypes from Jaba) of each of 17 populations of *dicoccoides* (listed in Table 1) were selected at random. Each of the genotypes was crossed with durum cv 'Langdon' (LDN). This cultivar has the standard chromosome arrangement, as has been shown by numerous crosses with 'Chinese Spring' wheat (Joppa and Williams 1988). A minimum of three F_1 plants of each cross were grown in 15-cm clay pots in a glasshouse. One or more spikes from each plant were sampled and fixed in Carnoy's Solution (6:3:1 ethanol:chloroform:glacial acetic acid). After 2 days at room temperature, the samples were transferred to 70% ethanol and stored at 4°C until examined.

Pollen mother cells (PMCs) were squashed in a drop of modified carbol fuchsin (Darlington and LaCour 1975). Cells at MI of meiosis were examined, and chromosome pairing in a minimum of 20 cells were recorded for each plant. Genotypes were considered to have a translocation if multivalents (excluding trivalents) were observed at MI of meiosis in one or more of the parent plants, or in one or more of their hybrids with LDN, and if the frequency of observed multivalents exceeded 4%. In this study, translocation frequency (TF) was defined as the total number of cells or genotypes with a translocation divided by the total number of cells or genotypes examined.

Identification of translocated chromosomes

One or two genotypes from 12 of the populations were crossed with a complete set of LDN D-genome disomic substitution lines (LDN-DS). These lines are disomic for a D-genome chromosome and nullisomic for a homoeologous chromosome (Joppa and Williams 1988). Two or more plants from each cross were grown in 15-cm clay pots in a glasshouse, sampled, and examined as in experiment one. The chromosomes involved in the translocations were determined from the pairing data. The non-critical crosses had one quadrivalent plus 11 bivalents plus two univalents at MI of meiosis. The critical crosses had one trivalent plus 12 bivalents plus one univalent at MI. In crosses that involved more than one translocation, the chromosomes involved could be determined, but not the chromosomes involved in individual translocations.

Each genotype of *dicoccoides* used in this study originated from a single plant selected at random from one of the populations. Many of the genotypes were examined cytologically, and any genotype that had PMCs with an average of more than 5% multivalents was considered to be a translocation heterozygote. Crosses of these plants with LDN produced some plants with multivalents and some plants with none. Thus, these genotypes must have been heterozygous for one or more translocations.

All genotypes that produced hybrids with multivalent frequencies greater than 0.04 were considered to carry translocations. Plants that produced lower frequencies of multivalents were considered to result from errors in counting or may have resulted from homoeologous pairing.

Statistical analysis

We used the SPSS (1990) statistical package for univariate and multivariate analysis (multiple regression) of the data. Translocation frequency in the investigated populations was used as the dependent variable in correlation analysis with ecogeographical and population variables. These variables were extracted from Table 1 of Nevo and Beiles (1989). Some of the values for temperature variables in this study have been corrected to conform with more detailed and precise data obtained since the previous publication.

Results

The genotypes of *dicoccoides* had from zero to as many as three quadrivalents in hybrids with LDN durum (Fig. 1f). Also, some hybrids had as many as 8 chromosomes in a

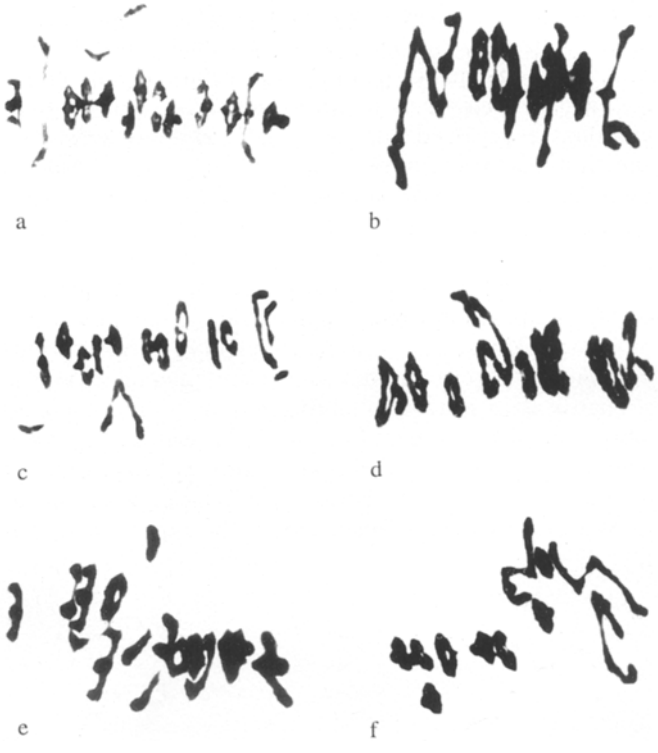

Fig. 1a–c Chromosome pairing in crosses between *T. dicoccoides* genotypes and the LDN-DS: **a** 13″+2′ in crosses without a translocation, **b** 1^{iv}+11″+2′ in non-critical crosses, **c** 1‴+12″+1′ in a critical cross. **d–f** Chromosome pairing in crosses of LDN and *T. dicoccoides* with other multivalents: **d** a cell with a chain of five and two univalents (2n=27), **e** a cell with an open quadrivalent and a complex ring of four, **f** a cell with three quadrivalents and 8 bivalents

Table 1 Frequency of quadrivalents and higher multivalents in PMCs of F_1 hybrids between 'Langdon' durum and several genotypes from each of 16 Israeli and 1 Turkish population of *dicoccoides* (*ND*=no data)

	Genotype												Population frequency
	1	2	3	4	5	6	7	8	9	10	11	12	
Population													
Mt. Hermon (1)	1.00	0.75	0.08	1.00	0.00	0.00	0.92	0.92	1.00	0.98	1.00	ND	0.818
Qazrin (5)	0.16	0.13	0.35	0.00	0.02	0.23	0.00	0.00	0.00	ND	ND	ND	0.444
Yehudiyya (7)	0.00	0.03	0.16	0.05	0.28	0.35	0.05	0.08	0.15	0.21	0.00	0.00	0.667
Gamla (8)	0.00	0.07	0.13	0.03	0.02	0.03	0.88	0.86	0.83	0.95	ND	ND	0.600
Rosh Pinna (9)	0.00	1.00	0.07	0.00	0.00	0.00	0.12	0.00	0.00	0.95	0.88	ND	0.455
Mt. Gilboa (16)	0.16	0.03	0.47[b]	0.08	0.17	0.02	0.15	0.05	0.30	0.25	1.00	ND	0.818
Gitit (18)	0.34	0.64	0.05	0.01	0.00	0.00	0.10	0.10	0.16	0.54	ND	ND	0.700
Kokhav Hashahar (19)	0.01	0.00	0.04	0.07	0.02	0.05	0.45	0.98	0.00	0.08	0.00	0.00	0.417
Bet Meir (22)	0.00	0.00	0.86	0.00	0.58	0.00	0.00	0.00	0.97	0.00	0.00	ND	0.273
Jaba (23)	0.45	0.51	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	1.000
Amirim (24)	0.00	0.03	0.95	0.05	0.92	0.00	0.90	0.00	0.42	0.35	ND	ND	0.600
Nahef (25)	0.39	0.00	0.12	0.13	0.05	0.00	0.13	0.56	0.09	0.00	ND	ND	0.700
Beit Oren (28)	1.00	1.00	1.00	0.95	0.95	1.00	1.00	0.99	0.96	1.00	1.00	ND	1.000
Daliyya (29)	0.50	0.35	0.22	0.41	0.38	0.50	0.20	0.40	0.38	0.40	ND	ND	1.000
Bat Shelomo (30)	0.94	0.15	0.25	0.05	0.11	0.17	0.08	0.96	1.00	0.99	0.84	ND	1.000
Givat Koach (33)	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.52	ND	ND	ND	1.000
Siverek (34)	0.34	0.00	0.00	0.44	0.03	0.15	0.22	0.10	0.11	1.00	0.00	ND	0.636

[a] Data from parental genotype; progeny plant did not receive a translocation
[b] Population frequency equals genotypes with more than 0.04 translocations divided by total genotypes

ring at MI of meiosis. All 17 populations had at least 1 genotype that differed from LDN by at least one translocation (Table 1).

There were 4 populations that had at least one translocation in all of the sampled genotypes. One of these, (Beit Oren, pop. 28) always had two translocations, and Givat Koach (pop. 33) had three translocations in 8 of the 9 sampled genotypes. Pairing frequencies were similar for each of the genotypes in pop. 28, but this does not prove that all had the same two translocations. For example, the 2 sampled genotypes from Jaba (pop. 23) had different translocations (Table 2).

There were hybrids from some populations that had very low frequencies of multivalent pairing, on the order of 2% to 4%. These frequencies may have resulted from pairing between non-homologous chromosomes. If these genotypes are excluded, the overall frequency of translocations in these populations was 0.70. This is much higher than the 0.21 reported by Kawahara et al. (1993). The data also differ from those of Kawahara for specific populations investigated in both studies.

Kawahara et al. (1993) did not find translocations in the population from Qazrin (pop. 5), but 4 of 9 genotypes (0.44) had translocations in our study. Conversely, the values for Mt. Hermon (pop. 1) are similar, 0.58 versus 0.82. Kawahara et al. (1993) examined 10-16 genotypes per population versus 9-12 in this study. In a few cases, both studies used the same genotypes, and a comparison of the data indicated that discrepancies were usually due to genotypes that this study found to be heterozygous for translocations. There were 20 genotypes from 8 populations that segregated for translocations. For example, the progeny of a single plant of genotype 7-32 included one plant with 14″ of chromosomes and one plant with 1^{iv}+12″. Both plants were crossed to LDN, and both F_1 progenies had a high frequency of multivalents. Thus, one plant was homozygous and one plant was heterozygous for a translocation.

The segregating genotypes were from 1 population from the center of the range of *dicoccoides* distribution in Israel, 4 from the mesic west margin of distribution, and 3 from the xeric north, east, and south margins. The *dicoccoides* genotypes that segregated for translocations were Mt. Hermon: 1-47, Yehudiyya: 7-16, 7-19, 7-32, Mt. Gilboa: 16-25, 16-29, Gitit: 18-56, Amirim: 24-49, Nahef: 25-30, 25-44, Daliyya: 29-9, 29-22, 29-31, 29-34, 29-42, and Bat Shelomo: 30-4, 30-15, 30-18, 30-20, and 30-44. But, this is a minimum estimate because we grew and investigated only a small number of plants of each genotype and a small number of hybrid plants from each cross.

Chromosomes involved in translocations

The differences in the frequency with which translocated chromosomes formed quadrivalents may be an indicator of the similarity of translocations in different genotypes within a population. For example, in Daliyya (pop. 29) all genotypes had similar pairing frequencies, while in many of the other populations, large differences were observed in the pairing between different genotypes. These differences may indicate that the translocations were not the same. Stebbins (1971) reported that observed quadrivalent frequencies in meiotic cells are affected by the length of the translocated segments of the respective chromosomes. Populations 8, 9, 16, 19, 24, and 30 each had at least two levels of quadrivalent frequency, and this suggests that each of these populations had at least two different trans-

Table 2 Chromosome pairing in F_1 hybrids between 'Langdon' D-genome disomic substitution lines and selected genotypes of *dicoccoides*

Langdon-DS line	*T. dicoccoides* genotypes[a]								
	Mt Hermon	Rosh Pinna		Jaba		Amirin	Beit Oren	Bat Shelomo	Givat Koach
	1-11	9-10	9-11	23-1	23-2	24-10	28-11	30-11	33-22
1D(1A)	1^{IV}+1″+2′[b]	1^{IV}+1″+2′	1^{IV}+1″+2′	1^{IV}+1″+2′	1^{IV}+1″+2′	1^{IV}+1″+2′	1^{IV}+1‴+10″+1	1^{IV}+1″+2′	1^{IV}+1″+2′
2D(2A)	–	1^{IV}+1″+2′	1^{IV}+1″+2′	1^{IV}+1″+2′	1‴+12″+1	1‴+12″+1′	2^{IV}+9″+2′	1^{IV}+1″+2′	1^{IV}+1″+2′
3D(3A)	–	1^{IV}+1″+2′	1^{IV}+1″+2′	1^{IV}+1″+2′	1^{IV}+1″+2′	1^{IV}+1″+2′	2^{IV}+9″+2′	1‴+12″+1′	1^{IV}+1″+2′[c]
4D(4A)	1^{IV}+1″+2′	1^{IV}+1″+2′	1^{IV}+1″+2′	1^{IV}+1″+2′	1^{IV}+1″+2′	1^{IV}+1″+2′	1^{IV}+1″+2′(3) 13″+2′(10)	1^{IV}+1″+2′	1^{IV}+1″+2′
5D(5A)	1^{IV}+1″+2′	1^{IV}+12″+1′	1^{IV}+1″+2′	1^{IV}+1″+2′	1^{IV}+1″+2′	1^{IV}+1″+2′	2^{IV}+9″+2′	1^{IV}+1″+2′	1^{IV}+1″+2′
6D(6A)	1^{IV}+1″+2′	13″+2′	1^{IV}+1″+2′	13″+2′	1^{IV}+1″+2′	1^{IV}+1″+2′	1^{IV}+1″+10″+1′	1^{IV}+1″+2′	1^{IV}+1″+2′
7D(7A)	1^{IV}+1″+2′	1^{IV}+1″+2′	1^{IV}+1″+2′	1^{IV}+1‴+10″ +1′(3) 1^{IV}+1″+2′(6)	1^{IV}+1″+2′	1^{IV}+1″+2′	2^{IV}+9″+2′	1^{IV}+1″+2′	1^{IV}+1″+2′
1D(1B)	1^{IV}+1″+2′	1^{IV}+1″+2′	1^{IV}+1″+2′	1^{IV}+1″+2′	1^{IV}+1″+2′	1^{IV}+1″+2′	1^{IV}+1‴+10″+1	1^{IV}+1″+2′	1^{IV}+1″+2′
2D(2B)	1^{IV}+1″+2′	1^{IV}+1″+2′	1‴+12″+1′	1^{IV}+1″+2′	1‴+12″+1′	1‴+12″+1′	2^{IV}+9″+2′	1^{IV}+1″+2′	1^{IV}+1″+2′
3D(3B)	1‴+12″+1′	1^{IV}+1″+2′	1^{IV}+1″+2′	1‴+1″+3′?	1^{IV}+1″+2′	1^{IV}+1″+2′	2^{IV}+9″+2′	1^{IV}+1″+2′	1^{IV}+1″+2′[c]
4D(4B)	1^{IV}+1″+2′	1‴+12″+1′	1^{IV}+1″+2′	1^{IV}+1″+2′	1^{IV}+1″+2′	1^{IV}+1″+2′	2^{IV}+9″+2′	1^{IV}+1″+2′	1^{IV}+1″+2′
5D(5B)	1‴+12″+1′	1^{IV}+1″+2′	1‴+12″+1′	1^{IV}+1″+2′	1^{IV}+1″+2′	1^{IV}+1″+2′	2^{IV}+9″+2′	1^{IV}+1″+2′	1‴+12″+1′
6D(6B)	1^{IV}+1″+2′	1‴+12″+1′	1^{IV}+1″+2′	1^{IV}+1″+2′	1^{IV}+1″+2′	1^{IV}+1″+2′	2^{IV}+9″+2′	1^{IV}+1″+2′	1‴+12″+1′
7D(7B)	1^{IV}+1″+2′		1^{IV}+1″+2′	1^{IV}+1″+2′	1^{IV}+1″+2′	1^{IV}+1″+2′	2^{IV}+9″+2′	1‴+12″+1′	1^{IV}+1″+2′
	3B/5B	4B/6B	2B/5B	7A?/3B?	2A/2B	2A/2B	1A/1B/6A/?	3A/7B	5B/6B

[a] Numbers in parentheses are number of cells observed
[b] 1′=one univalent, 1″=one bivalent, 1‴=one trivalent, 1^{IV}=one quadrivalent, etc.
[c] Tends to be desynaptic

locations. In a few cases we have further proof supporting this hypothesis.

A sample of 17 genotypes from 12 populations were crossed with a complete set of LDN-DS lines of durum wheat to determine the identity of the translocated chromosomes. The progenies of those crosses that did not involve a translocation produced hybrids that had 13″+2′ (Fig. 1a) at MI of meiosis. These included genotypes Qazrin: 5-51, 5-57; Yehudiyya: 7-34, 7-40; Kokhav Hashahar: 19-36, 19-46; Bet Meir: 22-37; and Siverek: 34-7. The hybrids with genotypes that contained translocations produced two types of pairing. The non-critical crosses produced hybrids that had 1^{IV}+11″+2′ (Fig. 1b), and critical crosses produced hybrids with 1‴+12″+1′ (Fig. 1c) at MI of meiosis.

There were 3 genotypes in pop. 9 (Rosh Pinna) with a very high frequency of cells with a quadrivalent. Two of these genotypes were crossed with the 14 LDN-DS lines. Genotype 9-30 had a 4B/6B translocation, and 9-55 had a 2B/5B translocation (Table 2). Cells of genotype 9-7 always had at least one multivalent and a frequency of 0.58 chains or rings of 8 chromosomes. The 9-27 genotype had a low frequency of multivalents (0.12). Thus, there probably were at least four different translocations in the sample of 11 genotypes from this population.

All 11 genotypes from Beit Oren (pop. 28) had two translocations. One of these genotypes (28-32) was crossed with the LDN-DS. The data indicates that chromosomes 1A, 1B, and 6A were involved in translocations, but the fourth chromosome could not be determined (Table 2). There were 2 genotypes from different populations that had a 2A/2B translocation, but this does not mean that they were the same. The two parent populations (Amirim and Jaba) are separated by 150 kilometers, and the chromosome arms or the location of the break points may be different. All of the other investigated translocations were different from each other (Table 2).

All of the B-genome chromosomes were involved in at least one translocation, and they were involved much more frequently than chromosomes from the A-genome. The B-genome chromosomes were also more frequently involved in translocations than had been observed for A-genome chromosomes in previous studies (Vega and Lacadena 1983). Except for 2A/2B, homoeologous chromosomes rarely were involved in the same translocation, suggesting that *dicoccoides* has a gene(s) that effectively prevents pairing between homoeologous chromosomes and that *Ph* genes were not responsible for the observed translocations.

Translocations: associations with climatic and geographic factors

Spearman rank correlation analysis (r_s) of translocation frequencies were calculated with the ecogeographical variables listed in Table 1 of Nevo and Beiles (1989). In addition, a variable (Frontier) was defined to indicate those populations at the periphery of the distribution of the species (Frontier=1); Frontier equals zero if the population is more centrally located. Thus, Frontier equals one for populations 1, 16, 18, 19, 23, 25, 28, 29, 30, and 33. This is based on the hypothesis expressed in the Discussion that translocations may help to generate new multilocus combinations that allow an extension of species distribution.

The water and temperature variables themselves were significantly negatively correlated (mean annual rainfall versus mean annual temperature, r_s=–0.58). The three temperature means (annual, January, and August) also were highly correlated among themselves (r_s=0.54 to 0.91).

Some of the populations (25, 28, 29, and 33) were listed as small and as having limited variability for allozymes in Nevo and Beiles (1989). Beit Oren (pop. 28) is exceptionally low in allozyme variability and is also relatively uniform for translocations. Although the fixation of the two translocations must reflect a selective process, it is plausible that the high TF may be influenced by the small population fixation process. The other populations show variability for TF and, therefore, the correlations with environmental variables were calculated with and without the data from Beit Oren.

Translocation frequencies and some environmental variables were significantly correlated as follows (the first value is with Beit Oren and the second without): (1) Rendzina soil type (r_s=0.454, P=0.067, n=17; r_s =0.497, P=0.050, n=16); (2) interannual variation in rainfall (r_s=–0.664, P=0.005, n=16; r_s=–0.613, P=0.015, n=15); (3) coefficient of variation in rainfall (r_s=–0.510, P=0.044, n=16; r_s=–0.437, P=0.103, n=15). The two significant rainfall climatic variables reflect the variation in annual rainfall between years (See Nevo and Beiles 1989 for explanation). The water availability parameters, annual humidity (r_s=0.609, P=0.009, n=17; r_s=0.540, P=0.031, n=16) and humidity at noon (r_s=0.639, P=0.008, n=16; r_s=0.574, P=0.025, n=15) also were correlated with TF. The first principal component of the eight water availability variables (representing 66% of the variance) was correlated with TF (r_s=0.606, P=0.013, n=16; r_s=0.582, P=0.023, n=15).

Multiple regression analysis to determine the best combination of predictors of TF were conducted. The three factors, annual humidity, humidity at noon, and rainfall variation coefficient were added to the equation one factor at a time. Annual humidity and TF had a highly significant correlation R^2=0.459 (P<0.01). The addition of humidity at noon increased R^2 to 0.521 (P<0.01), and the addition of rainfall variation coefficient gave a R^2 value of 0.617 (P<0.01). Removal of the Beit Oren population in the same order reduced R^2 as follows: 0.405 (P=0.011), 0.474 (P=0.021), and 0.592 (P=0.016), respectively. It is apparent that the removal of Beit Oren from the analyses did reduce, but did not have a major effect on, the significance of most correlations.

Thus, both Spearman rank correlations and multiple regression emphasizes the importance of water factors in determining TF distribution. However, the correlations are strongly influenced by the high TF (1.00) of the 3 populations near the coast and south of Haifa (pops. 28, 29, and 30). This area has an environment that is lower in temper-

ature, higher in moisture, and higher in humidity than most of the other studied environments.

We also explored the association between TF and population size. The population sizes vary from a few hundred plants to a few thousand plants, to tens or hundreds of thousands of plants (see Nevo and Beiles 1989). The Spearman rank correlation with population size was r_s=–0.537, P=0.026, n=17. Thus, translocation frequency increased as population size decreased.

The distribution of wild emmer is continuous in the central populations north of Lake Galilee (Golan Heights and Eastern Upper Galilee) and includes Qazrin, Yehudiyya, Gamla, and Rosh-Pinna. The remaining populations are marginal or peripheral. The latter are semi-isolated or isolated and much smaller and disjunct in their distribution. In this study, these marginal populations were divided into two climatic regions, the western margins (Amirim, Nahef, Beit Oren, Daliyya, and Bat Shelomo) and the xeric and mesic populations in the north, east, and south (Mt. Hermon, Kokhav Hashahar, Gitit, Mt. Gilboa, Bet Meir, Jaba, (all in Israel), and west of Siverek, in Turkey. The Mann Whitney non-parametric test was used to compare TF of marginal versus central populations. The mean rank of the 4 central populations was 5.13, and the mean rank of the marginal (xeric and mesic) populations was 10.19 (Mann-Whitney test of P=0.075). The non-parametric test suggests that marginal populations have a higher TF (TF=0.766, SE=0.70) than that found in the 4 central populations (TF=0.541, SE=0.055).

The 11 frontier populations had a mean TF of 0.826 as compared to 0.506 in the other 6 populations. The Mann-Whitney test was significant (P=0.006), and leaving Beit Oren out of the analysis had little effect on significance (P=0.009). Thus, TF appears to be structured and to display climatic, edaphic, and demographic associations in variably stressful margins of the distribution of wild emmer.

Discussion

The pervasive presence of translocations in these populations requires some explanation. Equally puzzling was the presence of numerous genotypes that were heterozygous for translocations, particularly in view of the high inbreeding rate of self-pollinated species such as wheat. Polymorphism and heterozygosity for translocations may be maintained in a population by one or several mechanisms: outcrossing (induced by sterility or other mechanisms), selection, or a high frequency of crossing-over between non-homologous chromosomes. The lack of translocations involving homoeologous chromosomes argues against high cross-over frequency as a cause of high TF.

Adjacent disjunction in translocation heterozygotes results in duplication deficiencies and in sterility (Burnham 1956); alternate disjunction results in normal gametes. Thus, if adjacent disjunction is frequent, sterility could result in increased outcrossing in plants with translocations. However, a comparison of seed set in a sample of genotypes with and without translocations indicated that there was no difference in the seed set of selfed spikes (data not presented). Also, Golenberg (1988) reported that outcrossing in *dicoccoides* is less than 1%, though outcrossing was shown to vary geographically in wild barley (*Hordeum spontaneum* Koch.) from the xeric south to the mesic north in Israel (Brown et al. 1978).

We conclude that outcrossing probably was not a factor in the maintenance of heterozygous translocations in these populations. The presence of heterozygous translocations in these populations could be the result of selection. Possibly, as in the classical studies of *Oenothera* by Cleland (1972), a favorable translocation reduces crossing-over in the critical areas of a chromosome(s) and leads to higher average fitness. This appears to be the case in most marginal populations. Furthermore, the climatic correlates of TF suggest that translocations may play a role in reducing crossing-over in wild emmer wheat in marginal as compared to central populations.

An alternative explanation is that a non-deleterious translocation persists in a population because it is not selected against. However, the demonstration that translocations are associated with ecogeography, i.e., climatic and demographic marginality factors, supports selection as the explanation for the maintenance of translocations. Similar conclusions have been reported by Kawahara et al. (1993). The maintenance of heterozygous translocations in some of the populations cannot be the result of random processes because it declines by 50% in each generation in self-pollinated species. One possibility is that the high TF in populations at the mesic periphery of the species distribution is related to disease resistance. Since, in general, fungal and bacterial diseases increase as humidity and rainfall increase, plant fitness is affected by climate and the fixation of disease resistance by a reduction in crossing-over due to translocations. But, we have no proof of this hypothesis.

It should be of great importance to further explore the possibility that translocations are associated with microgeographic and -climatic factors, mirroring the regional patterns of allozyme polymorphisms, as was earlier shown by Nevo (1988). A study of allozymes, disease resistance, plant morphology and translocation polymorphism in a large number of specific genotypes from both central and peripheral populations should be undertaken to elucidate these relationships.

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