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Geographical variation in heading traits in wild emmer wheat, *Triticum dicoccoides*. I. Variation in vernalization response and ecological differentiation

Received: 18 March 1996 / Accepted: 13 December 1996

Abstract Geographical variation in vernalization response and narrow-sense earliness was investigated for accessions of wild emmer wheat, *Triticum dicoccoides*, collected in Israel. Wide variation between and within populations was observed in both characters. The analysis of vernalization response showed that 2 accessions from Tabigha were of a strong spring growth habit, and thus wild emmer wheat was classified into four types, i.e., strongly spring type, moderately spring type, moderately winter type, and strongly winter type, according to their vernalization response. Whereas winter types were frequently found in most populations except that of Tabigha, the distribution of spring types was sporadic and restricted to warmer areas. It was thus suggested that spring type in *T. dicoccoides* might have evolved from a winter prototype as an adaptation to warmer conditions. Within moderately winter and moderately spring types, quantitative differences in vernalization response, measured as Dof_{70}/Dof_{20} and Dof_{20}/Dof_{0}, were observed between populations. Inter- and intra-population variation in vernalization response could be explained to some extent by the difference in growing conditions at each habitat. It was clearly indicated that environmental heterogeneity caused ecogenetic differentiation in wild emmer wheat in Israel. Wild emmer wheat also varied considerably for narrow-sense earliness, ranging from 32.9 days to 69.5 days among accessions. However, it was difficult to explain its geographical variation simply by a linear relationship with environmental factors, and a nonlinear relationship and/or unknown microgeographic heterogeneity may be responsible.

Key words Vernalization · Narrow-sense earliness · Adaptation · Ecological differentiation · *T. dicoccoides*

Communicated by J. W. Snape

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Introduction

Vernalization requirement is one of the most important characters affecting the adaptability of winter crops, and this character has been intensively investigated in cultivated hexaploid wheat (for reviews Flood and Halloran 1986 and Evans 1993). It plays an important role in the control of heading time and adaptation to low winter temperatures, as indicated by Kato and Yamashita (1991). As to the adaptation of tetraploid wheat, a survey of world collections revealed that most durum wheats were of a spring growth habit (Qualset and Puri 1974). Similar results were also obtained by Nakai and Tsunewaki (1967). As vernalization requirement is important for adaptation to low temperatures, the distribution of spring and winter types should relate to the growing conditions. The cultivation of tetraploid wheat is mainly restricted to autumn sowing in areas with mild winters or to spring sowing areas, and thus the predominance of the spring type may be a reflection of cultivation under relatively warmer conditions. However, archaeological evidence indicates that *Triticum dicoccum* was widely cultivated in the past (Bell 1987), when those adapted to colder areas might have been winter types. It is therefore suggested that the frequency of spring and winter types at the present time does not necessarily mean that emmer wheat has evolved from a spring type to a winter type.

The distribution of the wild progenitor of emmer wheat, *T. dicoccoides* L., is restricted to the areas around the Fertile Crescent, where winters are relatively mild.

Although the existence of intra-specific variation in heading time was reported by Nevo et al. (1984) and Tanaka and Sakamoto (1979), little is known about its constituent traits. Kushnir and Halloran (1982) observed intra-specific variation in vernalization response among five accessions representing two ecotypes in Israel, the center of genetic diversity for wild emmer (Nevo and Beiles 1989). This result indicated that genetic polymorphisms within and between populations involving spring and winter types were established in *T. dicoccoides* before the domestication of emmer wheat. However, as the number of accessions examined was small, it was difficult to demonstrate the extent of genetic variation in heading traits and to clarify the significance of adaptation for genetic differentiation within and between populations with diverse geographical origins in Israel.

In the study described here, therefore, intra- and inter-population variation in heading traits, i.e., vernalization response and narrow-sense earliness, were surveyed for wild emmer wheat accessions collected from various populations across the entire ecological spectrum of wild emmer in Israel. The importance of heading traits for the adaptation of wild emmer wheat is also discussed by taking the growing conditions at the respective habitats into consideration.

Materials and methods

Wild emmer wheat, *Triticum dicoccoides* L., sampled from 23 populations covering a wide range of growing conditions in Israel were used in this study. Detailed descriptions of the collection sites were described previously by Nevo and Beiles (1989), along with the climatic records. The number of accessions per population ranged from 8 to 21, and totalled 392 (Table 1). These accessions have been intensively studied for isozyme variation (Nevo et al. 1982; Nevo and Beiles 1989) and other characters (as reviewed by Nevo 1986, 1988, 1995). They were compared with 14 accessions of cultivated emmer, 8 of *T. dicoccum*, 5 of *T. durum*, and 1 of *T. turgidum*, which were supplied by the Plant Germ-plasm Institute, Kyoto University, Japan.

Vernalization response

All accessions were vernalized at 2°C for 0, 20, or 70 days. Seeds were sown in soil-filled containers at a spacing of 2.5 cm (between plants in a row) × 3 cm (between rows). The containers were transferred into a vernalization chamber under a 2°C and 24 h daylength regime and kept for 0, 20, or 70 days. Sowing time was adjusted to the treatment duration so that the three treatments would be completed

Table 1 Inter- and intra-population variation in growth habit, vernalization response, and narrow-sense earliness

Population	Total no. of accessions examined	Number of accessions (mean vernalization response)[a]				Narrow-sense earliness (mean ± SD)
		Strongly spring	Moderately spring	Moderately winter	Strongly winter	
North area						
Mt. Hermon	16	–	–	3 (57.05)	13	48.48 ± 6.96
Central area						
Qazrin	18	–	–	17 (81.79)	1	48.15 ± 2.86
Yehudiyya	20	–	15 (70.51)	5 (105.10)	–	42.12 ± 1.81
Gamla	16	–	15 (62.18)	1 (77.50)	–	40.79 ± 3.65
Rosh-Pinna	20	–	–	20 (85.07)	–	42.08 ± 1.83
Tabigha	19	2 (96.67)	17 (87.04)	–	–	49.50 ± 3.94
South area						
Mt. Gilboa	8	–	–	8 (92.29)	–	44.62 ± 2.93
Mt. Gerizim	18	–	–	18 (73.72)	–	41.58 ± 4.09
Gitit	15	–	7 (61.66)	8 (94.57)	–	42.85 ± 2.99
Kokhav Hashahar	18	–		18 (92.34)	–	50.01 ± 8.05
Taiyiba	15	–	–	14 (91.68)	1	46.98 ± 6.13
Sanhedriyya	15	–	–	15 (80.83)	–	52.83 ± 5.32
Bet-Meir	20	–	–	20 (124.26)	–	37.24 ± 2.77
J'aba	20	–	–	20 (94.23)	–	43.93 ± 2.94
West area						
Amirim	14	–	–	14 (88.48)	–	50.08 ± 4.13
Nahef	10	–	–	9 (79.86)	1	46.80 ± 2.11
Achihood	21	–	–	21 (70.88)	–	45.33 ± 2.49
Nesher	19	–	–	11 (79.97)	8	59.18 ± 5.68
Beit-Oren	19	–	–	19 (78.03)	–	42.06 ± 1.84
Daliyya	18	–	–	18 (75.86)	–	42.79 ± 3.51
Bat-Shelomo	16	–	2 (74.78)	14 (99.99)	–	44.39 ± 3.38
Yabad	19	–	–	19 (97.79)	–	48.71 ± 2.05
Givat-Koach	18	–	–	18 (101.91)	–	47.51 ± 1.24
Total	392	2	56	310	24	45.92 ± 6.13

[a] Vernalization response shown in parentheses was expressed as Dof_{20}/Dof_0 for spring types and as Dof_{70}/Dof_{20} for moderately winter types.

at the same time. Plants were then grown in a phytotron under a 20°C and 18 h daylength regime. The unfolding date of the flag leaf was recorded along with the final leaf number on the main stem. For each accession, four plants were allotted to a treatment.

For an evaluation of vernalization response, the criteria should include the number of days to flag leaf unfolding, and also reflect the growth increment achieved during vernalization treatment, as plant growth proceeds even under low temperature conditions. The growth increment can be measured as the decrease in the number of days to the first leaf unfolding after vernalization treatment, as indicated by Kato and Yamagata (1988). Therefore, vernalization treatment duration can be converted into the number of days which gives the corresponding growth at 20°C by regression analysis of the number of days to the first leaf unfolding after vernalization treatment using the treatment duration as an independent variable. The analysis of 4 randomly selected accessions of *T. dicoccoides* showed that the regression coefficient averaged − 0.171, and that 70 and 20 days in the vernalization chamber corresponded to 11.95 and 3.42 days in the phytotron, respectively. The converted values were added to the number of days to flag leaf unfolding after the vernalization treatment to give the number of days from germination to flag-leaf unfolding (Dof). The detail of the methodology for the measurement is fully described by Kato and Yamagata (1988).

Accessions which successfully unfolded their flag leaf by day 84 after sowing without vernalization treatment were regarded as spring types, and the others as winter types. Among the winter types, accessions which successfully unfolded the flag leaf with 20 days of vernalization were regarded as moderately winter types and the others as strongly winter types. Vernalization response of the spring types was measured as the percent reduction of Dof by 20 days of vernalization as compared with the non-treated control (represented as Dof_{20}/Dof_0). The vernalization response of moderately winter types was measured as Dof_{70}/Dof_{20}.

Narrow-sense earliness

Narrow-sense earliness was estimated by Dof of each accession measured in the above experiment. As mentioned above, Dof indicates how many days are necessary from germination to flag leaf unfolding if the wheat plants were grown at 20°C throughout the experiment. It should vary depending on temperature and daylength conditions. However, in the present study, all accessions were fully vernalized by 70 days of vernalization and thereafter grown under continuous illumination. Therefore, Dof_{70} shows the earliness of each accession, which is independent of vernalization response and photoperiodic response, and corresponds to narrow-sense earliness (Yasuda and Shimoyama 1965), which is also termed as earliness per se (Hoogendoorn 1985a). In conclusion, narrow-sense earliness was estimated by Dof_{70} for most accessions.

However, in some accessions, Dof_{70} became larger than Dof_{20} because flag leaf unfolding was delayed by an excessively prolonged vernalization treatment, as has been reported in common wheat by Derera and Ellison (1974) and Kato and Yamagata (1988). In such accessions, Dof_{70} should become larger than intrinsic narrow-sense earliness, and thus Dof_{20} is considered to be a better estimate of narrow-sense earliness. Therefore, narrow-sense earliness was estimated by Dof_{20} for those accessions whose Dof_{70}/Dof_{20} was larger than 1.

Results

Vernalization response

Of the accessions tested, 334 failed to unfold their flag leaf without a vernalization treatment, and 24 of others failed even after 20 days of vernalization. Therefore, 310 accessions were classified as moderately winter types and 24 as strongly winter types (Table 1). Among the moderately winter types, vernalization response measured as Dof_{70}/Dof_{20} varied considerably, ranging from 47.4% to 139.3%.

On the other hand, 58 accessions unfolded their flag leaves without vernalization treatment, and these could be classified as spring types (Table 1). The vernalization response of these accessions, measured as Dof_{20}/Dof_0, ranged from 50.5% to 97.2% (Fig. 1). In 2 accessions, 11-04 and 11-14, it was more than 96% and the difference between Dof_{20} and Dof_0 was statistically insignificant ($t = 1.87$, $df = 5$ for 11-04; $t = 2.00$, $df = 6$ for 11-14). This result indicates that Dof was not reduced by vernalization treatment and that these accessions have a strong spring growth habit whose existence has never been reported before in wild emmer wheat.

The frequency of the four types differed between populations ($P < 0.01$). Although moderately winter types were frequently found in most populations, except that of Tabigha, the distribution of strongly winter types was largely restricted to Mt. Hermon and Nesher (Table 1). On the other hand, spring types were mainly found in the low altitude populations around the Sea of Galilee. In Tabigha, where the altitude is close to sea level and the average January temperature is 13°C, all accessions were of a spring growth habit with 2 accessions showing a strong spring growth habit. Both spring and winter types were found in 4 populations, i.e., Yehudiyya, Gamla, Gitit, and Bat-Shelomo, clearly showing the existence of intra-population variation even in such an adaptively important character.

Vernalization response was also quantitatively different between populations (Table 1). For moderately winter types, it was uniformly less than 80% in the

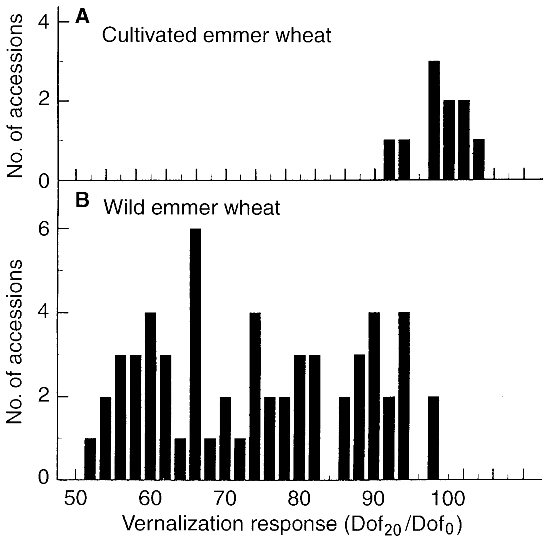

Fig. 1A, B Varietal variation in vernalization response, expressed as Dof_{20}/Dof_0 (%), among spring type accessions of cultivated (**A**) and wild (**B**) emmer wheat northern part of the western marginal area (Nahef, Achihud, Nesher, Beit-Oren, and Daliyya). If we consider that lower values of Dof_{70}/Dof_{20} indicate the need for a longer period of low temperature to achieve full vernalization, the vernalization requirement was relatively large in these populations. In contrast, it was nearly equal to or more than 100% in Yehudiyya, Bet-Meir, and the southern part of the western marginal area. The vernalization requirement was therefore relatively small in these populations and usually fulfilled by 20 days of vernalization treatment. Within spring types, similarly, vernalization response was different between populations, being larger in the lower altitude populations. Of the 5 populations where spring types were found relatively less sensitive types existed in the warmest site, Tabigha.

To analyze the adaptive significance of inter-population variation in vernalization response, we calculated Spearman rank correlations between vernalization response and ecogeographical variables. As shown in Table 2, the frequency of spring types correlated positively with mean annual temperature, and negatively with humidity and altitude, indicating that spring types usually adapted to warm, dry, low altitude areas. Among moderately winter types, vernalization response was correlated positively with temperature and evaporation, and negatively with moisture index, rainfall and latitude, indicating a smaller vernalization requirement occurred in warmer and drier areas than in the southern part of Israel or the Jordan valley.

Narrow-sense earliness

The accessions showed similar variation for narrow-sense earliness (Fig. 2), ranging from 32.9 days to 69.5 days in wild emmer wheat as compared to 35.4–75.9 days among the 14 accessions of cultivated emmer wheat. The difference between populations was statistically significant, ranging from 37.2 days (Bet-Meir) to 59.2 days (Nesher), as shown in Table 1. However, inter-population variation of narrow-sense earliness could not be associated with climatic differences and physical distances between populations. Intra-population variation also differed between populations, being larger in Mt. Hermon, Nesher, Kokhav-Hashahar, Taiyiba, and Sanhedriyya, where the range was more than 20 days.

Table 2 Spearman rank correlations of vernalization variables with ecogeographical variables in 23 populations of *Triticum dicoccoides* in Israel

Ecogeographical variables	Vernalization variables	
	Percentage of spring type	Vernalization response of moderately winter types
Longitude	0.372	– 0.239
Latitude	0.164	– 0.428*
Altitude (m)	– 0.478*	– 0.181
Mean Annual temperature (°C)	0.512*	0.356
Mean August temperature (°C)	0.372	0.586**
Mean January temperature (°C)	0.345	0.431*
Thornthwaite's moisture index	– 0.426	– 0.684**
Mean Annual rainfall (mm)	– 0.360	– 0.470*
Mean number of rainy days	– 0.116	– 0.467*
Mean humidity at 14:00 (%)	– 0.398	– 0.268
Mean annual humidity (%)	– 0.438*	– 0.195
Mean annual evaporation (mm)	0.181	0.532*

*,** Significant at 5% and 1% level, respectively

Discussion

Ecogeographical variation in vernalization response

The present study demonstrated that both qualitative and quantitative differences in vernalization response play an important role in the adaptation of *T. dicoccoides* and that key characters for adaptation are temperature and water conditions in each habitat (Table 2). The diverse ecotypes of *T. dicoccoides* found in Israel can be classified as follows. (1) A strongly winter ecotype prevails in the marginal northern area of Mt. Hermon, where it is cold, and on the north-facing slope of Mount Carmel, which is cool and humid. (2) In the central area, a large variation in vernalization response exists within and between populations. Spring types, including strongly spring types, occurred at a high frequency in Yehudiyya, Gamla, and Tabigha, where the altitude is less than 200 m and it is relatively warm and dry. At higher altitudes a large variation in vernalization response was observed among moderately winter type accessions. (3) Winter types having a large vernalization response adapted to low altitude and humid areas of the western marginals, while vernalization response was small in the southern part of this margin, Bat-Shelomo, Yabad, and Givat-Koach. (4) A large variation in vernalization response was

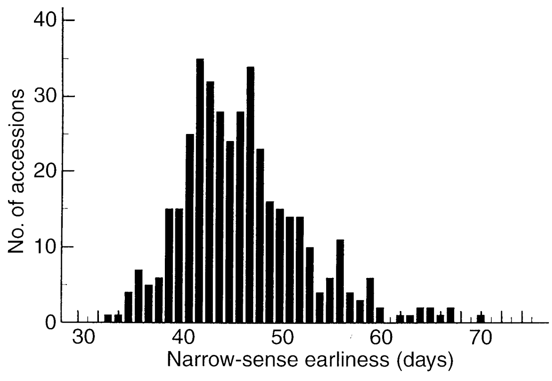

Fig. 2 Frequency distribution of narrow-sense earliness for wild emmer wheat accessions

observed within and between populations in the southern area, where it is extremely dry and rain fall is low.

Average January temperatures in Israel, except for Mt. Hermon, are over 8°C and not low enough to meet the vernalization requirement of winter types in common wheat. However, most of the *T. dicoccoides* accessions collected in Israel proved to be of winter growth habit (Table 1). Adaptation strategies must therefore be different between wild and cultivated wheats. As to the winter types of cultivated wheat, only 26.0% of the landraces unfolded their flag leaf when vernalized for 20 days (calculated from the data of Kato and Yokoyama 1992), and at least 40 days of treatment was required to achieve full vernalization. Their vernalization response (Dof_{70}/Dof_{20}) ranged from 48% to 68%. In contrast, for those of wild emmer wheat, more than 90% of the winter-type accessions unfolded the flag leaf by 20 days of vernalization (Table 1). Dof_{70}/Dof_{20} was more than 100% in one-third of the wild emmer wheats, indicating that these accessions were almost fully vernalized by 20 days of vernalization. It was therefore concluded that the vernalization requirement of winter types is generally smaller in wild emmer wheat, enabling adaptation to the relatively warm Israeli winters.

Distribution of spring types was restricted to 5 populations, at Yehudiyya, Gamla, Tabigha, Gitit, and Bat-Shelomo (Table 1). The average January temperature is more than 12.5°C at the latter 3 sites. If we consider that the effective temperature for vernalization is less than 11°C (Chujo 1966) or 9°C (Trione and Metzger 1970), any one of the winter types might not get fully vernalized at these sites, resulting in delayed flowering and often heat and/or aridity stress. Selection pressure would therefore favor the establishment of spring types in these populations. On the other hand, in Yehudiyya, the average January temperature is higher than in Qazrin (Nevo and Beiles 1989). From Yehudiyya to Qazrin there is a gradual rise in altitude of about 300 m, though these 2 sites are separated by only 8 km. Therefore, the difference in vernalization response between Yehudiyya and Qazrin could also be due to the microclimatic differences mainly related to altitude. A survey of isozyme genotypes (Golenberg and Nevo 1986) and genotypes for necrosis and chlorosis (Mori and Tsunewaki 1992) clearly showed that the frequency of each allele studied is completely different between the 2 populations. The establishment of respective ecotypes might result in the distinct genetic differentiation observed even over a short geographical distance.

Evolutionary change of vernalization response

In order to tolerate low winter temperatures winter crops must have vernalization requirement. It is thus suggested that the prototype of *T. dicoccoides* was of a winter growth habit and that spring types evolved as a result of adaptation to warmer winters. However, there are two controversial area of discussion. The first point is the direction of the mutation. Spring growth habit is a dominant character, and thus the above-mentioned evolutionary change should be possible only through a dominant mutation. Although the latters generally occurs less frequently than a recessive mutation, the important point is not the mutation rate itself but the adaptability of the mutant genes. For instance, adaptability was improved by spontaneous dominant mutations for reducing height in wheat (Konzak 1987) and for spring growth habit in barley (Takahashi and Yasuda 1970). The second point is the parallelism of the evolutionary change among *Triticum* and *Aegilops* species. Differentiation into spring and winter types is known in several diploid wild species, such as *T. boeoticum* (Nakai and Tsunewaki 1967) and several species of the *Sitopsis* section of the genus *Aegilops* (Tanaka 1954). These facts may indicate that the polymorphism observed in *T. dicoccoides* was derived directly from the ancestral species and was not acquired after the establishment of *T. dicoccoides*. On this basis, the geographically different distribution of spring and winter types could be explained as just being a result of adaptation to different climatic regimes. In such a case, clinal variation is usually observed for the key characters, like vernalization response of moderately winter types (Table 2), and thus spring types should be distributed more widely in various proportions which depend on the growing conditions. However, the distribution of spring types was sporadic, and a mixed stand of spring and winter types was observed only in 4 populations. Furthermore, strongly spring types were found in only 1 population. Therefore, it seems unlikely that the strongly and moderately spring types that existed at a lower frequency in the adjacent populations were selected for the adaptation to warmer winters. These results may support the idea that the spring type evolved from a winter prototype as an adaptation to warmer conditions (Kushnir and Halloran 1982; Flood and Halloran 1986).

A single major gene which seems to be homoeologous to *Vrn1* is known in *T. monococcum* (Kuspira et al. 1986) and in wild and cultivated emmer wheats (Tsunewaki 1962). In the present study, 2 accessions collected from Tabigha proved to be of a strong spring growth habit, indicating the existence of genetic variation in vernalization response within spring types. The variation could be genetically explained either by multiple allelism, which is known for the *Vrn1* locus in common wheat (Snape et al. 1976), or by allelic variation at an unknown locus that may be homoeologous to *Vrn2* located on chromosome 5B (Hoogendoorn 1985b; Kato et al. 1993). However, as the existence of the latter locus has not been confirmed in diploid and tetraploid species, further genetic analysis is necessary to elucidate the evolutionary change of growth habit in wheat.

Table 3 Differences in growth habit and vernalization response between two accession groups differing in narrow-sense earliness for two populations, Kokhav Hashahar and Nesher

Narrow-sense earliness[a]	Number of accessions and vernalization response	
	Kokhav Hashahar[b]	Nesher
Early	6 accessions moderately winter ($Dof_{70}/Dof_{20} \geqq 106$)	11 accessions moderately winter ($Dof_{70}/Dof_{20} \leqq 89$)
Late	11 accessions moderately winter ($Dof_{70}/Dof_{20} \leqq 98$)	8 accessions strongly winter

[a] Grouping criteria depends on the population:
Kokhav Hashahar; $37.4 \leqq$ early $\leqq 41.9$, $51.5 \leqq$ late $\leqq 59.5$
Nesher;$47.0 \leqq$ early $\leqq 58.2$, $61.6 \leqq$ late $\leqq 69.5$
[b] Narrow-sense earliness of 1 accession is missing

Narrow-sense earliness

Inter-population variation in narrow-sense earliness was observed between wild emmer wheat in the present study (Table 1). However, adaptation to an unpredictable climate generally makes the population structure heterogenous, especially for adaptively important characters such as maturing time, narrow-sense earliness and so on. Furthermore, narrow-sense earliness seems to be of a polygenic nature and exhibits a continuous variation. These facts clearly suggest that differentiation in narrow-sense earliness may not be so clear as for vernalization response. The difficulty in explaining the geographical variation simply by the overall meteorological data derives presumably from the two facts: (1) the data was not taken at each collection site, and (2) the regional climate interacts with local soil and topography.

Another interesting point is a character association between narrow-sense earliness and vernalization response, which was clearly demonstrated in 2 populations, Kokhav Hashahar and Nesher. As shown in Table 3, accessions with small and large narrow-sense earliness were characterized by small and large responses to vernalization treatment, respectively. In contrast to the above 2 populations, character associations were not clear in 3 populations, Mt. Hermon, Taiyiba, and Sanhedriyya, though a similarly large variation existed in narrow-sense earliness (Table 1). These results may also highlight the discussion on adaptation strategies in wild emmer wheat on both the macro- and microscales.

Acknowledgements We would like to thank Dr. S. Sakamoto, Professor of Ryukoku University, for kindly supplying the seeds of cultivated emmer wheat. The Israeli coauthors acknowledge the financial support of the Israeli Discount Bank Chair of Evolutionary Biology, and the Ancell-Teicher Research Foundation for Genetics and Molecular Evolution.

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