

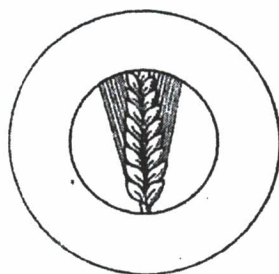


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Genomic distribution of domestication QTLs in wild emmer wheat, *Triticum dicoccoides*.

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ABSTRACT

Wild emmer wheat, *Triticum dicoccoides*, is the progenitor of modern tetraploid and hexaploid cultivated wheats. Our objective was to map domestication-related quantitative trait loci (QTL) and reveal their genomic distribution in *T. dicoccoides*. The studied traits include brittle rachis, heading date, plant height, grain size, yield, and yield components. A mapping population F₂/F₃ was derived from a cross between *T. dicoccoides* and *T. durum*. Approximately 70 domestication QTL effects were detected, non-randomly distributed among and along chromosomes. Based on the significant overlapping of map locations of QTLs underlying different domestication traits, seven *domestication syndrome factors* (DSF) were proposed, each affecting 5–11 traits. The DSFs are probably single pleiotropic genes or clusters of tightly linked genes that played a major role in the domestication process of *T. dicoccoides*. The genetic differentiation between cultivated wheat and its wild progenitor, displayed the following patterns: (i) clustering and strong effects of some QTLs; (ii) remarkable genomic association of strong domestication-related QTLs with gene-rich regions; and (iii) unexpected predominance of QTL effects in the A genome compared to the B genome. It seems that A genome may have played a more important role than the B genome during domestication evolution. The cryptic beneficial alleles at specific QTLs derived from *T. dicoccoides* may contribute to wheat and cereal improvement.

INTRODUCTION

Wild emmer wheat, *Triticum dicoccoides*, genome AABB, is a tetraploid, predominantly self-pollinating wild progenitor of modern tetraploid and hexaploid cultivated wheats (Zohary, 1970). *T. dicoccoides* proved important in wheat breeding in the past and it deserves in-depth future study as a potential genetic resource for cereal improvement (Nevo et al., 2002). Grass domestication evolution is the key for exploiting genome diversity for future cereal improvement. Analysis of quantitative trait loci (QTL) of domestication-related traits was studied in rice (Xiao et al., 1998), maize (Doebley et al., 1997), sorghum (Paterson et al., 1995), and millet (Poncet et al., 2000). The objective of this study was to analyze the genomic distribution of domestication QTLs in *T. dicoccoides*.

RESULTS AND DISCUSSION

The materials, phenotyping of domestication-related traits, genotyping of molecular markers, construction of molecular framework map, and QTL analysis methods were described in Peng et al. (2000, 2003) and Korol et al. (2001) (see also <http://esti.haifa.ac.il/~poptheor>). Approximately 70 domestication QTL effects were detected, non-randomly distributed

among and along chromosomes. The number of chromosomes with QTL effects for the specific traits ranged from two to eight. The number of detected QTL effects for specific chromosomes ranged from zero (chromosomes 1A, 3B, and 6A) to 19 (chromosome 5A), and more than half of the significant effects were located on chromosomes 1B, 2A, and 5A.

Domestication syndrome factors in wheat.

The map positions of QTLs for various traits on the same chromosome were highly overlapped. Most of the significant QTLs, referred to as "domestication syndrome factors" (DSFs) are clustered in limited intervals of chromosomes 1B, 2A, 3A, and 5A (Table 1). For almost all domestication-related traits, the number of QTL effects mapped on the A genome exceeded or equaled that on the B genome. Despite the high number of significant QTLs, they were highly clustered on the maps. Consequently, the total number of intervals of the QTL locations was 16; most of these clusters appear in pairs within the corresponding chromosomes (1B, 2A, 5A, 5B, 6B, 7A).

Table 1. Putative domestication syndrome factors (DSF) in wild emmer wheat, *T. dicoccoides*

DSF	Chr.	Involved QTL effects	Interval	Position (cM)
DSF1	1B	KNP, YLD, GWH, SNP, SWP	Xgwm273a-Xgwm403a	68.6 ± 8.8
DSF2	1B	KNP, KNS, KNL, YLD, SNP, SLS, SWP, SSW	Xgwm124-P57M52u	133.9 ± 22.8
DSF3	2A	KNP, KNS, YLD, HD, SNP, SWP, SNP, SWP	Xgwm630c-Xgwm294	150.8 ± 31.4
DSF4	2A	KNP, KNS, KNL, YLD, GWH, SLS, SSW, SWP	Xgwm294-Br	216.8 ± 11.8
DSF5	3A	KNP, KNS, KNL, YLD, SSW, SWP	Xgwm218-Xgwm638	148.1 ± 28.4
DSF6	5A	KNP, KNS, KNL, YLD, HT, SLS, SSW, SWP	Xgwm154-P56M50m	72.5 ± 12.6
DSF7	5A	all traits	Xgwm186-P56M53c	144.2 ± 29.3

Traits: kernel weight/plant (KNP); kernel number/spike (KNS); kernel number/spikelet (KNL); grain yield/plant (YLD); plant height (HT); spikelet number/spike (SLS); single spike weight (SSW); spike weight/plant (SWP); heading date (HD); 100-grain weight (GWH); spike number/plant (SNP).

A general transition from small-seeded plants with natural seed dispersal to larger-seeded nonshattering plants until harvest applies to all seed crops. These parallels transcend the deepest divisions within the angiosperms, with both monocot and dicot crops developing a similar adaptive domestication syndrome to human cultivation over the last 10,000 years (Harlan, 1992). Here, four of 14 chromosomes of tetraploid wheat harbored 80.4% of the 56 strong-to-moderate QTLs underlying the differences between wild *T. dicoccoides* and cultivated *T. durum* for 11 traits, clustered in seven intervals (Table 1). We propose seven domestication syndrome factors (DSFs), each involving a pleiotropic QTL or cluster of QTLs affecting five to 11 traits (Peng et al., 2003). Substantial clustering of domestication QTLs was revealed in sunflowers, and genomic regions influencing multiple traits harbored QTL with antagonistic effects (Burke et al., 2002). Morphological differences between maize and teosinte result from QTLs clustered in only five genomic regions (Doebley and Stec, 1993). Independent domestication of sorghum, rice, and maize involved convergent selection for large seeds, non-shattering spikes, and day-length insensitive flowering. These similar phenotypes are largely determined by a small number of QTLs that closely resemble each other in the three taxa (Paterson et al., 1995). Thus, our findings of a very limited number of DSFs corroborate the results in other cereal crops showing that the domestication syndrome is under a relatively simple and rapidly evolving genetic control (Paterson et al., 1995).

DSFs: linkage or pleiotropy.

We have previously demonstrated nonrandom distribution of molecular markers along chromosomes (Peng et al., 2000). It has been attributed to the non-randomness of crossover distribution along chromosomes, i.e., reduced recombination in the proximal regions and hotspots of recombination in the sub-telomeric regions of chromosome (Korol et al., 1994). The mechanism for QTL clustering may be the same as for molecular markers, i.e., tight linkage. If so, the coincidental mapping of several QTLs derives both from the small sample size effect on mapping resolution and scant recombination within blocks of QTL genes. Pleiotropy of the underlying genes could provide alternative interpretation. Coupling tight linkage and pleiotropy could better explain the data especially due to the high correlation between some traits. Factor analysis reveals that variation of the 11 traits can be represented by three "independent factors" accounting for 84% of the multiple trait variation. Thus, DSFs simultaneously affecting the traits that depend on more than one "independent factor" can indeed include tightly linked loci with pleiotropic effects on the considered traits. It is noteworthy, that the signs of the effects of the DSFs on different traits corroborated quite well with the correlations between the traits. Due to the small number (seven) of the revealed strong DSFs, it would be highly desirable to attempt further dissection of these factors by using the powerful multiple trait mapping (Korol et al., 2001) and special mapping designs based on accumulation of recombinants for the flanking markers and saturation of the target intervals by additional markers (Ronin et al., 2002).

DSFs and gene-rich regions.

Gene distribution in *Triticeae* chromosomes is highly nonrandom, with gene-rich regions alternating with gene-poor regions; like in other eukaryotes, gene-rich regions correspond to recombination hotspots (Gill et al., 1996; Faris et al., 2000; Kunzel et al., 2000). Remarkably, the map positions of all seven major wheat DSFs appeared to overlap with gene-rich regions (Peng et al., 2003). Therefore, high pleiotropy and/or tight linkage of most wheat domestication QTLs may suggest an important role of recombination in either consolidation of positive mutations within the DSF clusters (Korol and Iliadi, 1994; Otto and Barton, 1997) and/or reducing antagonism between artificial (directional) and background (purifying) selection. The presumed coincidence between DSFs and gene-rich regions and negative interference in the targeted regions (Peng et al., 2000) could facilitate dissection of these factors, their fine mapping, and finally, map-based cloning.

Relative importance of A and B genomes in domestication.

For 10 of the 11 domestication-related traits, the adjusted number of QTLs on the A genome generally exceeded that on the B genome (Peng et al., 2003). Thus, it seems that A genome has played a more important role than B genome in domestication of *T. dicoccoides*. However, interparental *Pst*I-based AFLP polymorphisms (Peng et al., 2000) showed that markers are not randomly distributed among A and B genomes of tetraploid wheat: about 60% of polymorphic AFLP loci were mapped to the B genome. Likewise, higher polymorphism in the B rather than in A genome applies to microsatellites (Röder et al., 1998) and RFLP markers (Liu and Tsunewaki, 1991) in common hexaploid wheat as well as in *T. dicoccoides* in Israel (Li et al., 2000). These nonrandom patterns may mirror the genetic differentiation of structure and function among the two genomes during domestication. Noteworthy, by screening the *GrainGenes* website (<http://wheat.pw.usda.gov/>) we found that out of 161 mapped wheat disease resistance genes 75 were from B genomes ($p < 0.008$), i.e. an opposite trend compared to distribution of domestication QTLs.

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