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Evolution of wild emmer wheat and wheat improvement.

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ABSTRACT

Wheats are important model organisms for testing evolutionary theory (both speciation and adaptation) and bread wheat is a major source of human nutrition (Nevo et al, 2002). Wheat speciation involves a polyploid series (2x, 4x, 6x). The origin of most wheats is wild emmer, *Triticum dicoccoides* (genome AABB) whose origin, center of diversity, and domestication sites are located in the Fertile Crescent, specifically in northern Israel (Galilee and Golan Mountains). In 1975, the Institute of Evolution at the University of Haifa, established a long-term multidisciplinary research program to study wild cereals including wild emmer, *T. dicoccoides*. The program includes evolutionary ecological-genetics and genomics coupled with the exploration of genetic resources for wheat improvement by genetic mapping and cloning. Both aspects, the theoretical and the applied, have proved to be of great importance for studying evolutionary theory and crop improvement (a list of publications can be found at: http://research.haifa.ac.il/~evolut.) Here, I will review the following perspectives of wild emmer wheat: the adaptive nature of genetic diversity resulting from natural selection; the unique population genetic structure and center of origin and diversity; genetic resources; and theoretical aspects including domestication evolution and applied aspects of wheat improvements both by classical breeding and modern biotechnology. Wild emmer wheat, probably the most important wild plant for human nutrition is a rich evolutionary model for understanding (and partly controlling) polyploid speciation and adaptation, and a mostly untapped, yet promising genetic resource for wheat improvement and increased food production.

INTRODUCTION

Wheats as Model Organisms. Wheats are important model organisms for testing various aspects of evolutionary theory (both for speciation and adaptation) and a major source of human nutrition. Wheat speciation involves a polyploid series (2x, 4x, 6x). The origin of most wheats is wild emmer, *Triticum dicoccoides* (genome AABB). In 1975, the Institute of Evolution at the University of Haifa, Israel, established a long-term multidisciplinary research program to study wild *T. dicoccoides*. The program includes evolutionary ecological-genetics and genomics coupled with the exploration of genetic resources for wheat improvement, genetic mapping, and cloning candidate genes. Both aspects, the theoretical and the applied, have proved to be of great importance for studying evolutionary theory and crop improvement (Nevo et al, 2002).

MATERIALS AND METHODS

This review is based on a collection of natural populations of wild emmer wheat, *Triticum*

dicoccoides, across their ecogeographic range in the Fertile Crescent from six countries, 38 populations, and 1650 genotypes in the Near East Fertile Crescent (Iran, Syria, Iraq -- primarily exchanged seeds), and Israel (33 populations), Turkey (four populations) and Jordan (one population). In addition, four microsite populations were examined for contrasting ecologies with different microclimates and soil types. The molecular markers (number of loci in parenthesis) used were allozymes (50), RAPDs (59), and microsatellites, i.e., SSRs (28). Likewise, some of the plants were evaluated agronomically and examined for abiotic (salinity, drought, and herbicides) and biotic (viral and fungal diseases) resistances.
Details on Materials and Methods appear in the individual papers cited here and appearing in Nevo et al (2002).

RESULTS

Genetic Diversity of Wild Emmer for Wheat Improvement. The molecular diversity and divergence of wild emmer wheat, *regionally* in the Near East Fertile Crescent, and *locally* in four natural populations at Qazrin, Ammiad, Tabigha, and Yehudiyya microsites in northern Israel display parallel ecological-genetic patterning. The *regional* and *local* results demonstrated significant spatial and temporal molecular diversity and divergence at the DNA and protein levels in *T. dicoccoides within* and *between* populations. Specifically, these patterns revealed that: (1) significant genetic diversity and divergence exist at single-, two-, and multilocus structures of allozymes, RAPDs, and SSRs over very short distances of several to a few dozen meters in the four microsites. (2) The genetic patterns across *coding* (allozymes) and partly *noncoding* (RAPDs and SSRs) genomic regions are correlated with, and predictable by environmental stress (*climatic, edaphic*, and *biotic*) and heterogeneity (the niche-width variation hypothesis), displaying significant niche-*specific* and *–unique* alleles and genotypes. (3) The genomic organization of wild emmer is *nonrandom, heavily structured*, and largely *adaptive*. It defies explanation by genetic drift, neutrality, or closely neutral models as the primary driving forces of wheat molecular evolution. The only viable model to explain the genomic organization of wild emmer is natural selection, primarily *diversifying, balancing and cyclical selection* over space and time according to the two- or multiple-niche ecological models. Spatial models are complemented with temporal models of genetic diversity and change (Kirzhner et al, 1996, 1999). Natural selection may interact with mutation, migration, and stochastic factors, but it overrides them in orienting wild emmer wheat evolutionary processes.

Based on mathematical modeling, we established that stabilizing selection with a cyclically moving optimum could efficiently protect polymorphism for linked loci, additively affecting the selected traits (Korol et al, 1994, 1996; Kirzhner et al, 1996). In particular, unequal gene action and/or dominance effects may lead to local polymorphism stability with substantial polymorphism attracting domain. Moreover, under strong cyclical selection, complex dynamic patterns were revealed including "supercycles" (with periods comprising hundreds of environmental oscillation periods) and "deterministic chaos" (Kirzhner et al, 1996; Korol et al, 1998; Ryndin et al, 2001). These patterns could substantiate polymorphism and increase the range of temporal variation of allele frequencies. We believe that this previously uncharacterized evolutionary mechanism may increase genetic diversity over long-term periods and contribute to overcoming massive extinctions.

Unique Population Genetic Structure and Center of Origin of Wild Emmer. Wheat Wild emmer wheat has a *unique ecological-genetic structure.* Its central populations in thecatchment area of the Upper Jordan Valley (eastern Upper Galilee and Golan Mountains) are massive and lush and represent its *center of origin and diversity*. However, southward in Israel and northward into Turkey, wild emmer becomes fragmented into *sporadic semi-isolated and isolated* populations that are characterized by an "*archipelago*" genetic structure in which alleles are built up locally in high frequency, but are often missing in neighboring localities. This phenomenon may even occur in the central continuous populations in which alternative fixation of up to eight alleles was described over tens to hundreds of meters in the Golan Heights between Qazrin and Yehudiyya (Nevo et al, 2002, pp. 75-77). The center of origin and diversity of wild emmer, the progenitor of most wheats, and that of other progenitors of cultivated plants is the Near East Fertile Crescent. Particularly in Israel with its extraordinary biotic and physical diversity, wild emmer developeda wide range of *adaptive diversity* to multiple diseases, pests, and ecological stresses both *within* and *between* populations, over a long evolutionary history. Most importantly, this diversity is neither random nor neutral. By contrast, it displays *adaptive genetic diversity* for *biochemical, morphological, and immunological* characteristics at all levels, which contribute to the species ability to adapt to widely diverse climatic and edaphic conditions by diverse and complex fitness syndromes. The long-lasting coevolution of wild emmer with parasites and the ecologically heterogeneous abiotic nature of Israel led to the development of *single multi-allelic* gene linkage disequilibria and *multi-locus* structures, *locally* and *regionally*, coadapted for both *short-* and *long-term* survival.

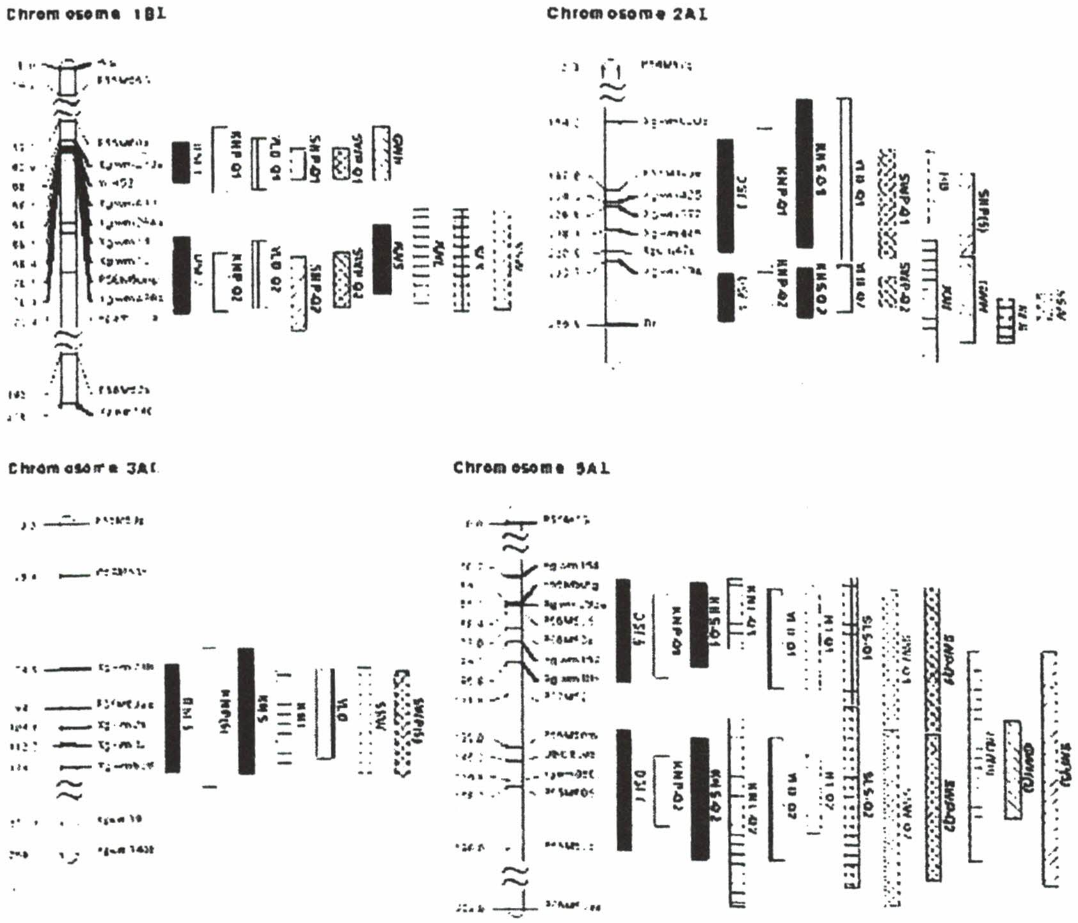

Figure. Map locations of DSFs (Domestication Syndrome Factors) and their involved QTLs (Quantitative Trait Loci) in L version maps of wild emmer wheat, *T. dicoccoides*. (Upper) Short arms of chromosomes. *(Right)* DSFs and corresponding QTLs: ☐, DSF; ■, KNS; ▤, kernel number/spikelet (KNL); ▥, YLD; ▨, HT; 王, spikelet number/spike (SLS); ▩, single spike weight (SSW); ▩, spike weight/plant (SWP); ☐, kernel weight/plant (KNP); ▤, HD; ▧, GWH; ▨, spike number/plant (SNP). The regular trait name represents a single QTL; the italic trait name represents a single QTL (Q2) detected by linked-QTL analysis; the regular trait name tailed with Q1 means the first QTL and tailed with Q2, the second QTL in a pair of linked QTLs. A tailed trait name (5) means that the QTL effect is not significant at the level of 5% of FDR but is significant at FDR 10%; (10) means that the effect is not significant at FDR 10%. (From Peng et al, 2003).

Genetic Resources. Wild emmer wheat is rich in genetic resources and is one of the best hopes for wheat improvement (Nevo, 2001). These include *abiotic* (e.g., drought, cold, heat, and salt resistances) and *biotic* (viral, bacterial, fungal, and herbicide resistances), high-quantity and -quality storage proteins (glutenins and gliadins), amino acids, amylase, and photosynthetic yield. Most of these resources are yet untapped and provide potential precious sources for wheat improvement. The current rich genetic map of *T. dicoccoides* with 549 molecular markers and 70 significant QTLs for 11 traits of agronomic importance (Peng et al, 2000, 2003), permit the unraveling of beneficial alleles of candidate genes that are otherwise hidden. These beneficial alleles could be introduced into cultivated wheat (simultaneously eliminating agronomically undesirable alleles) by using the strategy of marker-assisted selection. The genetic programs of wild emmer wheat conducted at the Institute of Evolution, University of Haifa, and elsewhere confirmed that *T. dicoccoides* is a very valuable wild germplasm resource for future wheat improvement. This program could highlight the evolution of wheat domestication and expedite the genomic analysis of wild relatives of wheat. It can thus provide a solid basis for *introgression* or *cloning and transformation* of agronomically important genes and QTLs from wild to cultivated wheats and for advancing wheat improvement (Figure). This is particularly important in view of the fact that the world's predicaments such as population explosion, widespread hunger, desertification and salinization are dramatically increasing, and limited water and fertile land resources are constantly threatened by environmental pollution and degradation.

Prospects. What will be the next step in wild emmer research in the genomic and post-genomic era? Conceptually, in-depth probing of comparative genome structure and function are the major challenges, in particular, the intimate relationship of the *coding* and *noncoding* genomes, primarily gene regulation. Such studies will unravel genome evolution and highlight the rich genetic potentials for wheat improvement residing in wild emmer wheat and wheat relatives including *Triticum* and *Aegilops* species as well as other Triticeae.

Specifically, we could divide the prospects, somewhat arbitrarily, into *theoretical* and *applied* perspectives (Nevo et al, 2002).

Theoretical Perspective.

1. Highlighting the genetic genome *structure, function, regulation*, and *evolution* at *macro-* and *micro*geographic scales of natural populations, bridging multilocus marker structures with fitness-related traits in order to get direct estimates of the adaptive fitness differentiation *within* and *between* populations (by using transplant experiments, mapping analysis (Figure), microarray methodology, and selection-based mapping of fitness components over the entire life cycle). (2) Exposing the genome organization of *T. dicoccoides* using molecular sequence analysis and molecular cytogenetic methods in order to probe the structure and interactions of the *nuclear, mitochondrial*, and *chloroplast* genomes. (3) Analysis of the genetic system, or the "transmission system," which determines the genetic flexibility of the species in diverse ecological contexts including: (a) Breeding system (reaction norm and genetic variation of the outcrossing rate). (b) Mutation rate in different elements of the genome. (c) Recombination properties of the genome, their genetic and ecological control. (d) Genomic distribution of structural genes, primarily *abiotic* and *biotic stress* genes, and their regulation function. (e) Interface between ecological and genomic spatiotemporal dynamics and adaptive systems. (f) Genome evolution in the polyploidization process. (g) Domestication evolution.

Applied Perspective.

1. Genetic fine-mapping and dissection of the collected *unique* genetic resources of agricultural importance by molecular markers and sequencing followed by introgression of the detected genes/alleles into elite cultivars via marker-assisted selection. (2) Molecular

cloning of adaptation genes based on integrated genomic strategies and novel methodologies including genetic and physical mapping, molecular markers, expressed sequence tags (EST), mapping, cloning and sequencing, microarray expression analysis, and genetic transformation of the defined target genes/alleles. (3) Comparative genetics/genomics of cereal plants aimed at deciphering the common and specific ways of domestication evolution (Figure).

REFERENCES

Kirzhner, V., Korol, A.B. and Nevo, E. 1996. Complex dynamics of multilocus systems subjected to cyclical selection. *Proceedings of the National Academy of Sciences, USA*, 93: 6532-6535.

Kirzhner, V., Korol, A.B. and Nevo, E. 1999. Abundant multilocus polymorphisms caused by genetic interaction between species on *trait-for-trait* basis. *Journal of Theoretical Biology*, 198: 61-70.

Korol, A.B., Preygel, I.A. and Preygel, S.I. 1994. *Recombination, Variability and Evolution: Algorithms of estimation and population-genetic models.* Chapman & Hall, London, pp. 361.

Korol, A.B., Kirzhner, V.M., Ronin, Y.I. and Nevo, E. 1996. Cyclical environmental changes as a factor maintaining genetic polymorphism. 2. Diploid selection for an additive trait. *Evolution*, 50: 1432-1441.

Korol, A.B., Kirzhner, V.M. and Nevo, E. 1998. Dynamics of recombination modifiers caused by cyclical selection: Interaction of forced and auto-oscillations. *Genetic Research*, 72: 135-147.

Nevo, E. 2001. Genetic resources of wild emmer, *Triticum dicoccoides*, for wheat improvement in the third millennium. *Israel Journal of Plant Science*, 49: 77-91.

Nevo, E., Korol, A.B., Beiles, A. and Fahima, T. 2002. *Evolution of Wild Emmer and Wheat Improvement. Population Genetics, Genetic Resources, and Genome Organization of Wheat's Progenitor*. Springer, pp. 364.

Peng, J., Korol, A.B., Fahima, T., Röder, M.S., Ronin, Y.I., Li, Y.C. and Nevo, E. 2000. Molecular genetic maps in wild emmer wheat, *Triticum dicoccoides*: Genome-wide coverage, massive negative interference, and putative quasi-linkage. *Genome Research*, 10: 1509-1531.

Peng, J.H., Ronin, Y.I., Fahima, T., Röder, M., Nevo, E. and Korol, A.B. 2003. Domestication quantitative trait loci in Triticum dicoccoides, the progenitor of wheat. *Proceedings of the National Academy of Science, USA*, 100: 2489-2494.

Ryndin, A., Kirzhner, V., Nevo, E. and Korol, A.B. 2001. Polymorphism maintenance in populations with mixed random mating and apomixes subjected to stabilizing and cyclical selection. *Journal of Theoretical Biology*, 212: 169-181.