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Commentary

SNPing *Aegilops tauschii* genetic diversity and the birthplace of bread wheat

Towards the end of second world war, McFadden & Sears (1946) published a lengthy and classic paper on the origin of hexaploid or bread wheat. In the appendix to this paper they acknowledged that Kihara (1944) had also independently identified *Aegilops tauschii* (syn. *Ae. squarrosa*, *Tritcum tauschii*) as the D-genome donor of bread wheat. Since then, there have been many studies on the taxonomy, biology, and genetics of this grass to seek answers to many questions, including the center of genetic diversity of *Ae. tauschii* and the place of origin of bread wheat. In this issue of *New Phytologist*, a paper by Wang *et al*. (pp. 000–000) is a culmination of these efforts and in many respects is a landmark contribution. It is a triumph of high-throughput genomics. They used 7,815 previously mapped (Luo *et al*., 2009, and unpublished), single nucleotide polymorphisms (SNPs) providing complete coverage of the genome to interrogate 402 accessions of *Ae. tauschii*, 75 hexaploid wheats, and seven tetraploid wheats using an Illumina Infinium Platform. But before delving deeper into their findings, let me fill in the key findings of the intervening period.

> *'… an arms race may have primed not only the resistance gene evolution but also the birth of hexaploid wheat in Caspian Iran …'*

Kihara & Tanaka (1958) made extensive collections of *Ae. tauschii* in the 1950's and, based on morphology, described subspecies *eusquarrosa* varieties *typica*, *anathera*, and *meyeri*, and subsp. *strangulata*. Kihara *et al*. (1965) also described extensive physiological specialization based on resistance to rust races and evidence of incipient speciation based on the sterility in F1 hybrids among individuals from different populations. Later work, with molecular markers, mainly isozymes and storage proteins (reviewed in Wang *et al*.), indicated that subsp. *strangulata* was the probable D-genome donor of bread wheat and Caspian Iran and/or Armenia as the center of diversity and origin of *Ae. tauschii*.

In a first application of DNA-based, RFLP marker analysis of genetic diversity, Lubbers *et al*. (1991) identified two genetically diverse groups, one consisting of subsp. *eusquarrosa* vars. *typica* and *anathera*, and another of subsp. *strangulata* and subsp. *eusquarrosa* var. *meyeri*. The analysis strongly supported the Caspian Sea region as the center of genetic diversity and origin of *Ae. tauschii*. The practical aim of this study was to identify genetically diverse *Ae. tauschii* accessions for direct introgression into bread wheat (Gill & Raupp, 1987) to enrich the genetically impoverished D genome of bread wheat (Kam-Morgan *et al*., 1989). The *Ae. tauschii*-derived materials had a huge worldwide impact on wheat crop improvement (Gill *et al*., 2006).

Returning to *Ae. tauschii* genetic diversity studies, Dvorak *et al*. (1998), in a large study of RFLP markers, confirmed the existence of two genetically diverse groups in *Ae. tauschii,* which crosscut taxonomic groupings but surprisingly proposed Armenia as the center of genetic diversity and origin of bread wheat.The current paper from his lab has revisited this question and, from SNP analysis, they conclude that, in fact, southwestern

Caspian Iran is the center of genetic diversity. Because they included a large number of wheat accessions in the analysis, they also have pinpointed the center of origin of bread wheat in Caspian Iran.

Wang *et al*. indicate a remarkable genetic differentiation of *Ae. tauschii* populations into S-1 and S-2 (mainly *strangulata* but also includes other forms) and T-1 and T-2 (mainly *tauschii* but may include other forms) gene pools occupying distinct habitats and geographic regions. There appears to be little genetic exchange between the two gene pools. The S-1 populations are restricted to Transcaucasia between 400–1500 m above sea level; the S-2 to the southwestern to eastern Caspian region at elevations of 25 m or less. The T-1 and T-2 populations are found only at high elevations, 400–3000 m above sea level. T1 is distributed in Transcaucasia, Turkey, and western Iran. T2 is found mainly in central Iran, Afghanistan, and eastward extending into China.

The S2 populations in Caspian Iran are morphologically and genetically diverse, and came into contact with cultivated teraploid emmer wheat, and produced hexaploid wheat through spontaneious hybridization. Surprisingly, of the 12 accessions most closely related to the wheat D genome, only one is of the *stranguata* type. Recently, some workers had proposed the independent origin of hexaploid wheat in Turkey (Giles and, Brown 2006), but the analysis reported here provides no evidence for this hypothesis.

Intriguingly, Wang *et al*. reported intermediate populations between the S and T pools near Ramsar, Iran, a region of tremendous genetic diversity for resistance to leaf rust, and also evidence that *c*. 4% of the wheat D genome is derived from the T gene pool. This region is where the Lr21 (a major gene providing resistance to leaf rust pathogen Puccinia triticina, a plague of wheat since Roman times) was postulated to have arisen from hybridization between two susceptible *Ae. tauschii* accessions, each carrying haplotypes H1 and H2, via a rare intragenic recombination event that produced a functional Lr21 gene of chimeric origin (H1H2 haplotype) (Huang et al., 2009). Both H1 and H2 haplotypes were also found in leaf rust susceptible hexaploid wheats, and from the F2 progeny of an H1/H2 hybrid, Huang et al. reconsituted the resistant Lr21(H1H2) locus. Huang et al. (2009) postulated that for such a rare recombinant resisting leaf rust to survive and spread over a large area in the Caspian region, strong selection pressure on *Ae. tauschii* weedy populations must have been exerted by leaf rust epidemics brought about by a susceptible wheat crop. One can also argue that a rare wheat hexaploid also would be selected if it survived leaf rust epidemics. Thus, an arms race may have primed not only the resistance gene evolution but also the birth of hexaploid wheat in Caspian Iran from hybrid swarms of susceptible tetraploid wheat with leaf rust resistant *Ae tauschii* strains.

Wang *et al*. also analyzed the patterns of genetic diversity among wheat chromosomes and arms. Chromosome 5D was found to be the genetically least diverse and 1D and 2D were found to be highly polymorphic. This observation again relates to the fact that chromosomes 1D and 2D are hotspots where many resistance genes have been mapped (Gill *et al*., 2008). Most genetic diversity was localized to the ends of chromosomes and was correlated with high recombination rates. Previously, deletion bin mapping had provided compelling evidence for the restriction of recombination and genetic novelty to the ends of chromsomes (Qi *et al.*, 2004; See *et al*. 2006).

This paper by Wang *et al*. will be of great interest to plant breeders who need to choose the most diverse *Ae. tauschii* accessions for genetic introgression into wheat. Is this the last word on the orgin of the wheat D genome? Probably not, but now that we are homing in to the place where bread wheat originated, perhaps a more thorough sampling of these regions or previously collected samples from these areas may provide additional data. More powerful genetic diversity tools, such as genotyping-by-sequencing, are coming on board, stay tuned!

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Key words: *Aegilops tauschii*, Caspian Iran, D-genome donor, genetic diversity, plant breeding, RFLP markers.