

Commentary

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

Towards the end of World War II, 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*, *Triticum 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. 925–937) is a culmination of these efforts and in many respects is a landmark contribution. It is a triumph of high-throughput genomics. They used 7815 previously mapped (Luo *et al.*, 2009), 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 1950s 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 laboratory 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 and 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. T-1 is distributed in Transcaucasia, Turkey, and western Iran. T-2 is found mainly in central Iran, Afghanistan, and eastward extending into China.

The S-2 populations in Caspian Iran are morphologically and genetically diverse, and came into contact with cultivated tetraploid emmer wheat, and produced hexaploid wheat through spontaneous hybridization. Surprisingly, of the 12 accessions most closely related to the wheat D genome, only one is of the *strangulata* type. Recently, some workers proposed the independent origin of hexaploid wheat in Turkey (Giles & 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.* (2009) reconstituted 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 chromosomes (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 origin 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!

Acknowledgements

This work was supported by the Kansas Agricultural Experiment Station and grants from the Kansas Wheat Commission and the US Department of Agriculture Special Research Grant to B.S.G. This is Kansas Agricultural Experiment Station journal article no. 13-276-J.

Bikram S. Gill

Wheat Genetics Resource Center, Department of Plant Pathology,
Throckmorton Plant Sciences Center, Kansas State University,
Manhattan, KS 66506-5502, USA
and
Faculty of Science, Genomics and Biotechnology Section,
Department of Biological Sciences, King Abdulaziz University,
Jeddah 21589, Saudi Arabia
(tel +1 785 532 1391; email bsgill@k-state.edu)

References

- Dvorak J, Luo MC, Yang ZL, Zhang HB. 1998. The structure of the *Aegilops tauschii* gene pool and the evolution of hexaploid wheat. *Theoretical and Applied Genetics* 97: 657–670.
- Giles RJ, Brown TA. 2006. GluDy allele variations in *Aegilops tauschii* and *Triticum aestivum*: implications for the origins of hexaploid wheats. *Theoretical and Applied Genetics* 112: 1563–1572.
- Gill BS, Friebe B, Raupp WJ, Wilson DL, Cox TS, Sears RG, Brown-Guedira GL, Fritz AK. 2006. Wheat Genetics Resource Center: the first 25 years. *Advances in Agronomy* 85: 73–135.
- Gill BS, Huang L, Kuraparthi V, Raupp WJ, Wilson DL, Friebe B. 2008. Alien genetic resources for wheat leaf rust resistance, cytogenetic transfer, and molecular analysis. *Australian Journal of Agricultural Research* 59: 197–208.
- Gill BS, Raupp WJ. 1987. Direct genetic transfers from *Aegilops squarrosa* L. to hexaploid wheat. *Crop Science* 27: 445–450.
- Huang L, Brooks S, Li W, Fellers J, Nelson J, Gill BS. 2009. Evolution of new disease specificity at a simple resistance locus in a weed–crop complex: reconstitution of the *Lr21* gene in wheat. *Genetics* 182: 595–602.
- Kam-Morgan LN, Gill BS, Muthukrishnan S. 1989. DNA restriction fragment length polymorphisms: a strategy for genetic mapping of D genome of wheat. *Genome* 32: 724–732.
- Kihara H. 1944. Discovery of the DD-analyser, one of the ancestors of *Triticum vulgare*. *Agriculture and Horticulture (Tokyo, in Japanese)* 19: 13–14.
- Kihara H, Tanaka M. 1958. Morphological and physiological variation among *Aegilops squarrosa* strains collected in Pakistan, Afghanistan and Iran. *Preslia* 30: 241–251.
- Kihara H, Yamashita H, Tanaka M. 1965. *Morphological, physiological, genetical, and cytological studies in Aegilops and Triticum collected in Pakistan, Afghanistan, Iran. Results of the Kyoto University scientific expedition to the Korakoram and Hidukush in 1955. Volume 1*. Kyoto, Japan: Kyoto University.
- Lubbers EL, Gill KS, Cox TS, Gill BS. 1991. Variation of molecular markers among geographically diverse accessions of *Triticum tauschii*. *Genome* 34: 354–361.
- Luo MC, Deal KR, Akhunov ED, Akhunova AR, Anderson OD, Anderson JA, Blake N, Clegg MT, Coleman-Derr D, Conley EJ *et al.* 2009. Genome comparisons reveal a dominant mechanism of chromosome number reduction in grasses and accelerated genome evolution in Triticeae. *Proceedings of the National Academy of Sciences, USA* 106: 15780–15785.
- McFadden ES, Sears ER. 1946. The origin of *Triticum spelta* and its free-threshing hexaploid relatives. *Journal of Heredity* 37: 81–89, 107–116.
- Qi LL, Echalié B, Chao S, Lazo GR, Butler GE, Anderson OD, Akhunov ED, Dvorak J, Linkiewicz AM, Ratnasiri A *et al.* 2004. A chromosome bin map of 16,000 expressed sequence tag loci and distribution of genes among the three genomes of polyploid wheat. *Genetics* 168: 701–712.
- See DR, Brooks SA, Nelson JC, Brown-Guedira GL, Friebe B, Gill BS. 2006. Gene evolution at the ends of wheat chromosomes. *Proceedings of the National Academy of Sciences, USA* 103: 4162–4167.
- Wang J, Luo M-C, Chen Z, You FM, Wei Y, Zheng Y, Dvorak J. 2013. *Aegilops tauschii* single nucleotide polymorphisms shed light on the origins of wheat D-genome genetic diversity and pinpoint the geographic origin of hexaploid wheat. *New Phytologist* 198: 925–937.

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