

Convergence within divergence: insights into wheat adaptation from *Triticum* population sequencing

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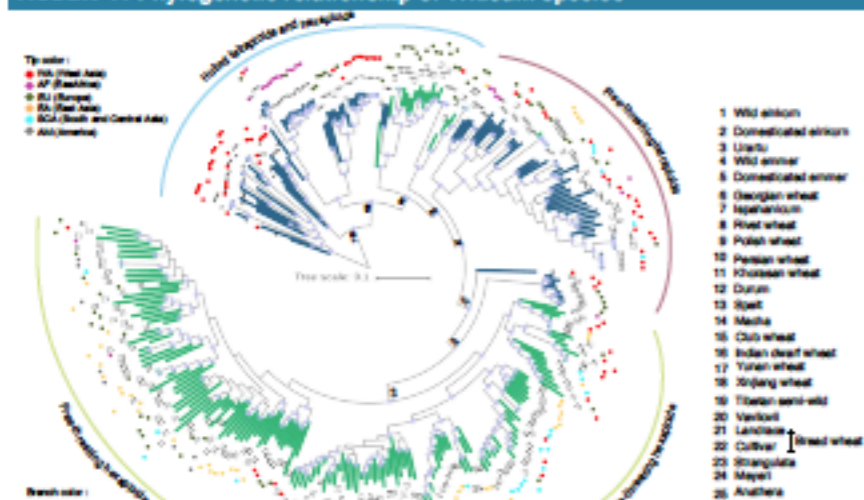


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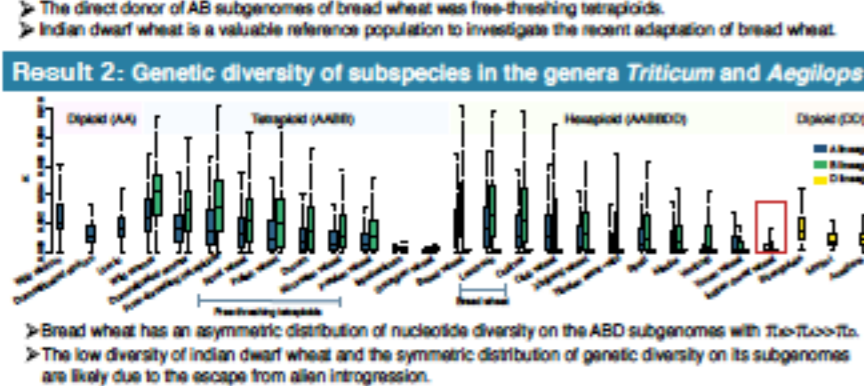
Abstract

Bread wheat expanded its habitat from a core area of the Fertile Crescent to global environments within ~10,000 years. The genetic mechanisms of this remarkable evolutionary success are not well understood. By whole-genome sequencing of populations from 25 subspecies within the genera *Triticum* and *Aegilops*, we identified composite introgression from wild populations contributing to a substantial portion (4–32%) of the bread wheat genome, which increased the genetic diversity of bread wheat and allowed its divergent adaptation. Meanwhile, convergent adaptation to human selection showed 2- to 16-fold enrichment relative to random expectation—a certain set of genes were repeatedly selected in *Triticum* species despite their drastic differences in ploidy levels and growing zones, indicating the important role of evolutionary constraints in shaping the adaptive landscape of bread wheat. These results showed the genetic necessities of wheat as a global crop and provided new perspectives on transferring adaptive success across species for crop improvement.

Result 1: Phylogenetic relationship of *Triticum* species



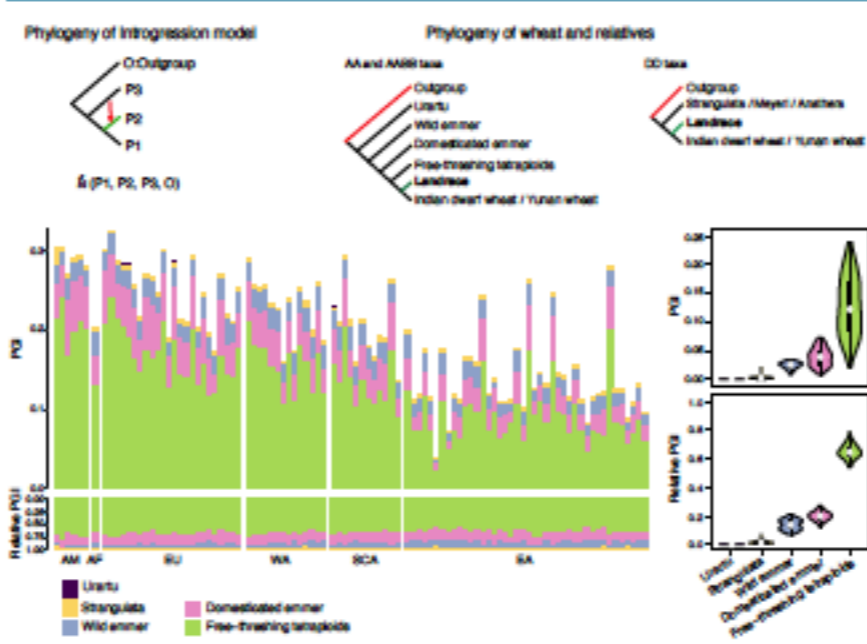
Result 2: Genetic diversity of subspecies in the genera *Triticum* and *Aegilops*



> Bread wheat has an asymmetric distribution of nucleotide diversity on the ABD subgenomes with $\pi_{AB} > \pi_{DD} > \pi_{D}$.

> The low diversity of Indian dwarf wheat and the symmetric distribution of genetic diversity on its subgenomes are likely due to the escape from alien introgression.

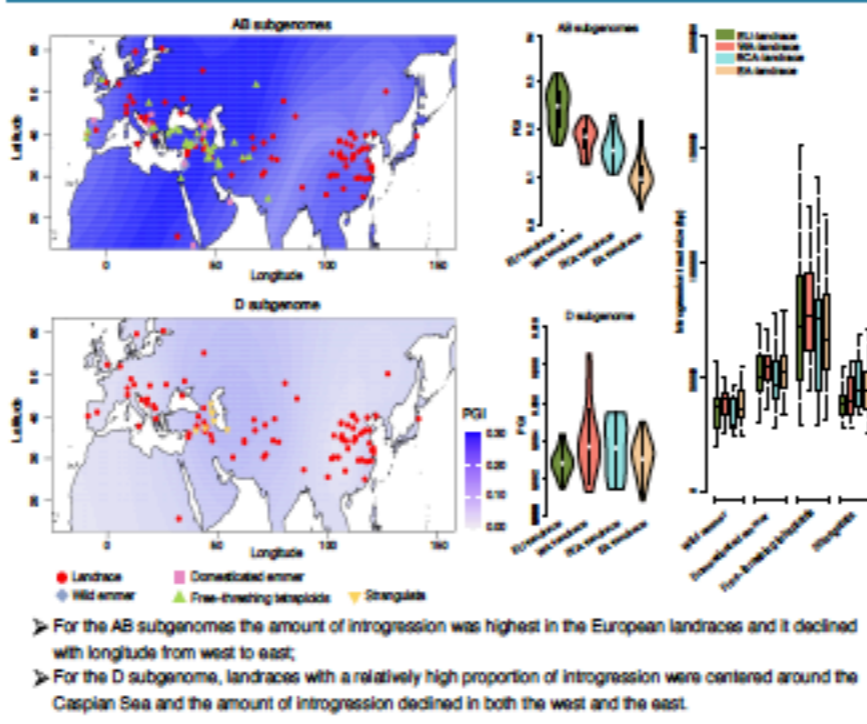
Result 3: Magnitude of alien introgression in bread wheat



> A high level of introgression in bread wheat, where the proportion of genome introgression (PGI) ranged from 3.82% to 32.08%, with a mean value of 19.45%.

> Compared with diploids, tetraploids dominated alien introgression in bread wheat.

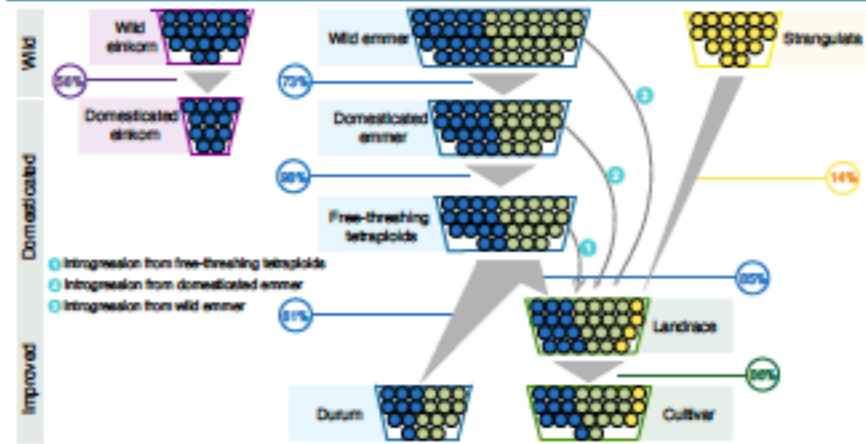
Result 4: Spatiotemporal dynamics of introgression in bread wheat



> For the AB subgenomes the amount of introgression was highest in the European landraces and it declined with longitude from west to east.

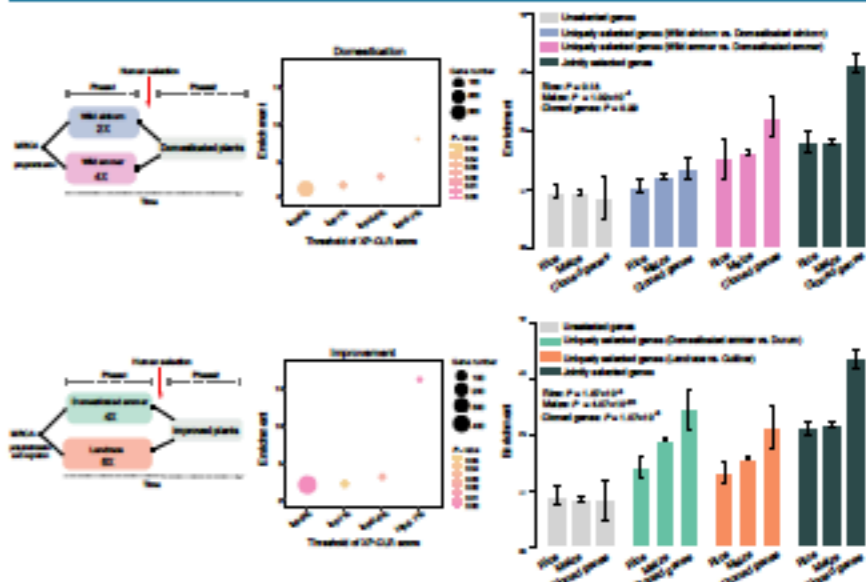
> For the D subgenome, landraces with a relatively high proportion of introgression were centered around the Caspian Sea and the amount of introgression declined in both the west and the east.

Result 5: The shift of genetic diversity of *Triticum* species



Despite the severe genetic bottlenecks of hexaploidization and domestication, the genetic diversity of bread wheat was largely compensated by composite gene flow from multiple groups of AABB taxa, including free-threshing tetraploids, domesticated emmer and wild emmer.

Result 6: Convergent adaptation of wheats to human selection



> Convergent adaptation to human selection in wheats and cereal crops.

> Everaging evolutionary constraints and transferring adaptive success across species for crop improvement.

Conclusions

> In this study, we took wheat as a model and performed the first genus-level whole-genome sequencing analysis in crops. The comprehensive sampling of *Triticum* species and the ultrahigh marker density ensured a robust phylogeny of *Triticum*.

> We found that about 4%–32% of bread wheat genome was directly contributed by introgressions; furthermore, increase of genetic diversity from alien introgression is fundamental to the global expansion of bread wheat.

> We identified significant footprints of convergent adaptation to breeding selection in wheats, which highlights the evolutionary constraints of wheat adaptation to human selection.

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