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Role of Targeted Recombination for Rapid Genetic Gains in Crop Improvement

*R. S. Parmar[1] and Sonali B. Chaudhari[2]
[1]Associate Professor and Head, Dept. of GPB, College of Agriculture, Junagadh Agriculture University, Motabhandariya-Amreli (365610), India
[2]Assistant Professor, Dept. of Soil Science, College of Agriculture, Junagadh Agriculture University, Motabhandariya-Amreli (365610), India
*Corresponding Author's email: rakeshparmar@jau.in

Plant breeding relies on crossing over (CO) to create novel combinations of alleles needed to confer increased productivity and other desired traits in new varieties. The evolution of plant genetics and breeding concepts has simplified the selection of superior, true-to-type lines. Despite significant advancements in DNA marker-based selection, plant breeders still largely rely on random meiotic events for generating variation (Ru and Bernardo, 2019). Given the probabilistic nature of creating desirable traits, the need for larger populations in breeding programs remains inevitable. Food security can be addressed through a combination of genetic improvements, optimized agronomic practices, and supportive policy measures, accelerating genetic gains remains one of the most impactful and practical strategies (Varshney *et al*., 2021). Global climate change is a leading aspect threatening agricultural productivity worldwide, along with the challenges of meeting the food requirements of the world's expanding population. Increased variations in rainfall and raised global temperature, along with increasing unpredictability in growing conditions, have caused the emergence, changed distribution and prevalence of pests and diseases. Abiotic and biotic stresses and loss of agricultural land caused by climate changes have direct or indirect negative impacts on agricultural production, usually causing yield losses (Yu *et al*., 2021).

Targeted Recombination

Targeted recombination refers to having recombination at specific marker intervals where they could lead to the largest genetic gain (Bernardo, 2017). Targeting recombination to specific chromosome loci rather than increasing it genome-wide holds significant potential. Modeling studies suggest that optimizing recombination breakpoints could enhance genetic gains for polygenic traits like yield by up to 15%. Though current understanding of quantitative trait loci (QTL) effects is limited, these findings highlight the utility of crossover targeting. In crops such as tomato, Arabidopsis, and maize, CRISPR/Cas9 has been used to induce double-strand breaks (DSBs) in somatic tissues, leading to COs via non-homologous end joining (NHEJ) or homologous recombination (HR). Alternatively, a dead Cas9 protein fused with SPO11 can target DSBs during meiosis, which has successfully increased CO rates in yeast. Another approach involves suppressing COs in specific chromosome regions. CRISPR-induced chromosomal inversions have redirected COs toward telomeres, potentially offering more complex control over crossing over distribution. These strategies demonstrate the potential for reshaping recombination landscapes to achieve higher genetic gains in plant breeding.

Modelling the Impact of Targeted Recombination

Modeling the effect of targeted recombination in maize demonstrated its potential to reduce linkage drag during incorporation of beneficial loci. By increasing COs six fold or twentyfold at the flanks of a donor chromosome segment, linkage drag was significantly reduced, leading to a faster return to the recurrent parent genome and a quicker removal of the donor genome. Targeting COs to a 1 Mb interval containing the donor locus yielded similar results, but was not more efficient than targeting only the flanks (Epstein *et al*., 2023). The overall CO rate increase had a greater impact on linkage drag than the specific targeting approach. While highly effective for introducing a few well-defined loci, targeted recombination may be limited in scalability for large numbers of loci. Nonetheless, it matches the efficiency of a tenfold global CO increase, suggesting its utility in improving breeding outcomes.

Rapid Bulk Generation Advancement (RBGA)

The RBGA scheme involves a structured process for breeding wheat with improved agronomic traits and disease resistance. In first year simple crosses are made in a controlled field screen house and F_1 to F_2 generations are bulked and advanced in the same screen house within the same year. In year 2 The F_3 populations are planted in the Toluca field, where plants with the desired agronomic traits and disease resistance (especially for yellow rust and *Septoria tritici* blotch) are selected. Individual spikes are harvested and chosen for grain quality, and head rows are planted in Obregon for further selection of agronomic traits and disease resistance (leaf rust and stem rusts). In the third year seed multiplication of best-performing lines with good grain traits. These lines undergo phenotyping for resistance to diseases, while simultaneous genotyping allows genomic selection by estimating genomic estimated breeding values (GEBV) using historic training set.. All trial data is used to select the best candidate parental lines for the next breeding cycle, based on their breeding values (Singh *et al*., 2022)

DNA Double-Strand Breaks

DNA DSBs play a critical role in shaping plant genomes, occurring either spontaneously or due to external factors like ionizing radiation or genotoxic agents. While DSBs can lead to severe damage such as chromosome loss or cell death, their repair is essential for maintaining genome integrity. There are two primary pathways for DSB repair: NHEJ and HR. NHEJ is error-prone, often resulting in small insertions or deletions (indels), and is the dominant repair mechanism in somatic cells. HR, on the other hand, is more precise and typically uses a homologous sequence for repair, though it is less common in somatic tissues. Various tools are used to induce DSBs, including meganucleases, transposon excision, and custom-designed nucleases like zinc-finger nucleases (ZFNs), TALENs, and CRISPR-Cas9. These tools allow for targeted mutagenesis and genome engineering, with CRISPR-Cas9 proving particularly efficient in a wide range of plant species (Filler Hayut *et al.,* 2017) Although techniques like UV-induced mutagenesis have been used for decades to induce DSBs, the introduction of CRISPR-Cas9 has brought precision to this process (Sadhu *et al*., 2016). For instance, CRISPR has been used to fine-map loci in yeast with high confidence, reducing the number of individuals to be screened while increasing the accuracy of identifying the desired region. This approach has been extrapolated to field crops like maize, where targeted recombination was shown to potentially increase breeding efficiency by over 200%. Similar success has been demonstrated in crops like soybean, wheat, pea, and barley, where targeted recombination across fewer chromosomes achieved equal or greater genetic gains compared to natural recombination. The genetic bottlenecks impose on our current crop varieties by the long breeding selection process. Consequently, they have removed most of the beneficial genetic diversity available for breeding and make further improvement of elite varieties by conventional breeding techno-logies a cumbersome process (Hickey *et al.* 2019).

Potential of Targeted Recombination for Enhanced Genetic Gains in Maize

CRISPR technology has enabled targeted recombination in yeast, prompting an investigation into its potential benefits in plants. Using genome-wide marker effects in two maize experiments, targeted recombination points were identified to maximize genetic gains. In the intermated B73 × Mo17 maize population, targeted recombination predicted a 15.3% yield gain, compared to 7.1% with non-targeted recombination, resulting in a relative efficiency of 212%. Across various traits and maize crosses, predicted efficiency ranged from 105% to 600%. These results suggest that targeted recombination could significantly enhance selection gains in maize, warranting further empirical validation.

Conclusion

While targeted recombination is still largely theoretical, its potential in improving genetic gains is significant. However, practical application requires further refinement of methodologies and overcoming challenges such as population-specific targets and potential trade-offs between traits. In this context, selection indices can help prioritize recombination targets. Plant breeders may need more time to assess the cost effectiveness of these techniques, specifically to calculate the “return on investments” before committing significant investment into these modern methods. Additionally, selection of appropriate selection methods is crucial for the continuous genetic gains for traits of interest. Ultimately, targeted recombination could be a valuable tool, particularly in marker-assisted backcross breeding, to reduce linkage drag and the population size needed for screening, leading to higher crop genetic gains.

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