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Unlocking the harvest index ceiling in maize: the *HI1-BRR1* module as a molecular valve for high-density and climate-resilient agriculture

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ABSTRACT

The harvest index (HI) has remained stagnant in modern maize despite decades of breeding efforts. Recent work by Guo et al. published in *Cell* identifies the *HI1-BRR1* regulatory module as a "molecular valve" governing source-sink carbon and nitrogen allocation. This commentary highlights the engineering significance of this discovery, emphasizing its potential to overcome the yield plateau imposed by high-density planting and environmental stresses. We also discuss how integrating this module into hybrid breeding programs, combined with precision nutrient management, can drive the next generation of "smart" maize cultivars tailored for high-efficiency agricultural systems.

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1 Introduction: from morphological improvement to physiological optimization

The harvest index (HI), defined as the fraction of photosynthates allocated to grain, was the cornerstone of the Green Revolution in wheat and rice. Semi-dwarfing genes (sd-1, *Rht*) enhanced lodging resistance and HI by altering plant architecture. However, maize followed a divergent path. Modern yield gains rely heavily on increased biomass accumulation under high-density planting rather than improved partitioning efficiency[1–5]. Guo et al.[6] address this "black box" by identifying a conserved regulatory module that fine-tunes source-sink dynamics at the molecular level-a critical step toward engineering crops for optimal resource distribution.

2 From the green revolution to the molecular era: unlocking the HI in maize

The HI represents how efficiently a plant turns biomass into grain. During the Green Revolution, semi-dwarfing genes dramatically increased HI of wheat and rice by over 60%. That single change doubled yields[7–12]. However, HI of maize was

already around 0.5 by the 1930s and has barely budged since. Despite its agronomic importance and high heritability, no HI QTL had been molecularly cloned before this study. That left a critical gap in our understanding of how assimilate partitioning is genetically controlled.

Guo et al.[6] systematically compared HI across maize evolution. The average increased from 0.26 in teosinte to 0.42 in landraces and 0.52 in modern lines, representing an 81% increase during domestication. Using two independent maize-teosinte BC_2S_3 populations, they identified 20 HI QTLs, five of which were consistently co-localized across populations. The maize alleles at all loci consistently increased HI, indicating strong directional selection during domestication.

Fine-mapping of the major QTL *HI1* on chromosome 1 narrowed it to a ~54-kb interval. The only candidate gene in this interval showed no detectable expression; instead, the functional target turned out to be BRR1, a B-type response regulator that located 22 kb downstream. Its expression is driven by a 9.1-kb enhancer that interacts with the promoter through long-range chromatin interactions. This enhancer was already present in teosinte (56.4%) and rose to 99.4% in landraces under strong selection. It is now fixed in modern maize.

3 *HI1-BRR1* module orchestrates

The elegance of this mechanism lies in CONZ1's dual role. It binds the *HI1* enhancer and *BRR1* promoter, and recruits GCN5 to stitch them into a chromatin loop. This loop boosts local H3K27 acetylation and opens up chromatin, thus activating *BRR1* transcription. Once activated, BRR1 orchestrates source-to-sink allocation by directly activating genes involved in carbon (C) and nitrogen (N) metabolism and transport. These targets include sugar transporters (*ZmSWEET13a*, *ZmSWEET4b*), N assimilation enzymes (*ZmNR1*, *ZmGLN2*, *ZmGOGAT2*), and an amino acid transporter (*ZmAAP48*). Isotope tracing of ^{13}C and ^{15}N confirmed that BRR1 is essential for moving both C and N from leaves and stems to developing ears during post-silking stage. In *brr1* mutants, those resources stay trapped in vegetative tissues, and dry matter remobilization plummets from ~10% to nearly zero. BRR1 also activates florigen genes *ZCN8* and *ZCN12*, linking reproductive timing with resource allocation.

The *HI1-BRR1* module marks an important advance in maize HI research. This module works through two angles: it coordinates source-sink relations and triggers reproductive development. The dual functions make it promising for high-density, high-yield breeding. But a key question remains: does it affect harvest index primarily through C-N partitioning, or by reducing sink capacity via ear differentiation? To sort out the cause-and-effect and timing between these two possibilities, we need isotope tracing and gene expression data from the ear differentiation stage. That should be a priority in follow-up studies.

4 *HI1-BRR1* module drives physiological domestication for enhanced yield and nitrogen use efficiency in maize

The translational potential of this discovery is compelling. In multiple environments across Tieling, Sanya, and Beijing, *BRR1* overexpression delivered stable yield increases of 10%–16%, coupled with improved HI and biomass. Importantly, grain protein, stalk strength, and lodging resistance remained at control levels. Under N-limiting conditions, *BRR1*-overexpressing lines yielded 28% more than wild-type controls. That gain was much larger than under normal N conditions. Based on China's maize sown area of approximately 44.67 million hectares in 2025, if this module is widely adopted, every 10% increase in adoption would boost grain output by roughly 10 million tons. This suggests that the module boosts N use efficiency, a trait that sustainable agriculture urgently needs. These findings indicate that *BRR1* does not merely redistribute existing photosynthates but elevates whole-plant C and N utilization efficiency.

Beyond its agronomic value, this work also changes how we think about maize domestication. Classic genes like *tb1* mainly affect plant shape and flower structure. *HI1-BRR1*, in contrast, reveals a "physiological domestication" route that reshapes internal source-sink relationships. The co-improvement of morphology and physiology may explain why maize achieved a high HI early in domestication, while other cereals did not. This also makes *BRR1* a valuable genetic resource for green high-yield breeding and resource-efficient agriculture.

5 Engineering implications and future perspectives

The discovery of *HI1-BRR1* offers transformative opportunities for agricultural engineering and breeding technology (Fig. 1).

Designer Hybrids for Precision Agriculture: Integrating *HI1-BRR1* with genes controlling plant architecture (e.g., *RAVL1* for compact stalks) and flowering time can produce ideotypes suited for mechanized harvesting and high-density regimes. Marker-assisted selection or CRISPR-based editing of the 9.1-kb enhancer provides a precise toolset for introgressing this trait into elite germplasm.

Enhanced N Use Efficiency: With global emphasis on reducing synthetic fertilizer inputs, the module's ability to improve N remobilization is vital. Engineering crops with optimized BRR1 activity could reduce nitrate leaching and lower the C footprint of maize production.

Climate Resilience Engineering: Extreme weather disrupts photosynthesis (source) while grain filling (sink) demands energy[13]. The BRR1-mediated "molecular valve" buffers against such disruptions by prioritizing resource allocation to the grain. Future research should explore stacking BRR1 with stress-responsive transcription factors to develop "stress-bypass" varieties that maintain HI under drought or heat stress.

Digital Phenotyping Integration: The specific expression patterns of *BRR1* can serve as biomarkers for high-throughput phenotyping platforms. Drones or ground robots equipped with hyperspectral sensors could monitor the "openness" of this molecular valve in real-time, allowing for dynamic adjustments in irrigation and fertilization strategies.

6 Conclusions

The *HI1-BRR1* module represents a paradigm shift from morphological to physiological breeding. As a tunable molecular valve, it addresses the fundamental challenge of source-sink imbalance in high-density cropping systems.

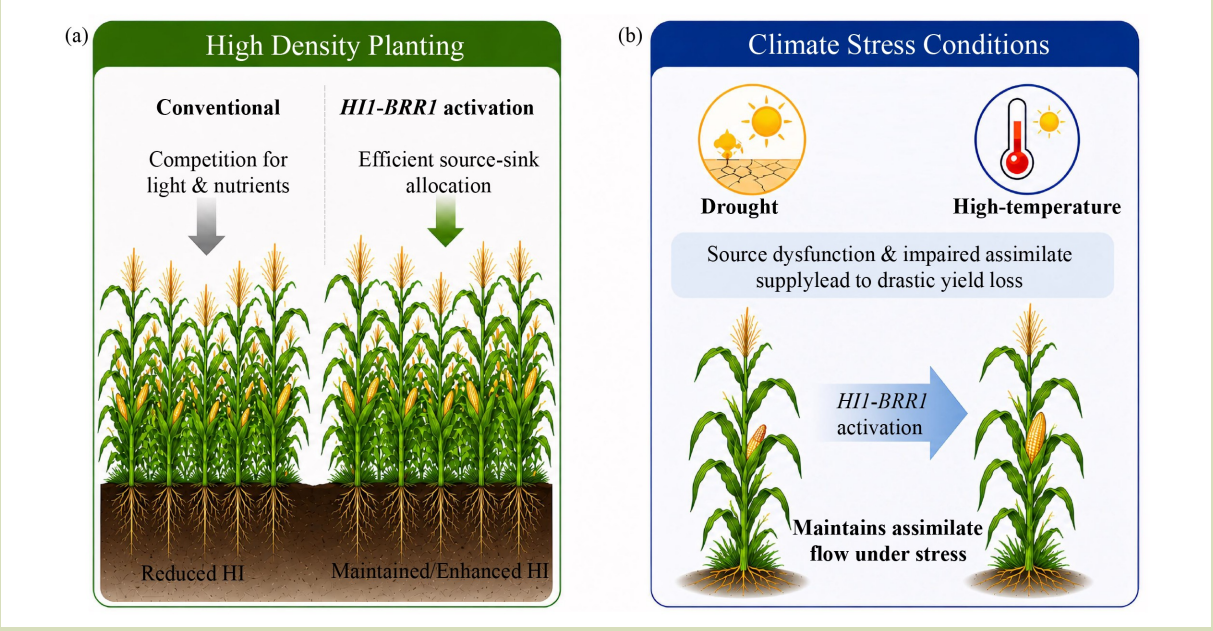


Fig. 1 Proposed model of the *HI1-BRR1* module in engineering high-yield maize. (a) Under high-density planting, the module maintains assimilating flow to grains despite shading and competition. (b) Under abiotic stress (drought/heat), the module prioritizes resource allocation to reproductive sinks, protecting harvest index. Integration with architectural genes (e.g., RAVL1) creates ideal plant types for future agriculture.

Translating this discovery into field-ready cultivars will require close collaboration between molecular biologists and agricultural engineers to optimize planting densities, nutrient regimes, and harvest logistics. Ultimately, this work provides a robust genetic toolkit to meet the dual challenges of global food security and environmental sustainability.

Compliance with ethics guidelines

Pengshuai Yan, Guohua Mi, Xuejun Liu, and Wen-Xue Li declare that they have no conflicts of interest or financial conflicts to disclose. This article does not contain any studies with human or animal subjects performed by any of the authors.

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