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Golden Genes: Breeding Maize for Higher Vitamin A Content

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Maize (*Zea mays* L.) is a globally important cereal crop and a major source of energy for millions of people, particularly in developing countries. However, conventional maize varieties are deficient in provitamin A carotenoids, leading to widespread vitamin A deficiency (VAD), a public health problem in many regions. The advent of biofortification—through conventional breeding, molecular marker-assisted selection, and transgenic approaches—has revolutionized efforts to enhance the nutritional value of maize. The discovery and utilization of key "golden genes" such as psy1 (phytoene synthase), lcyE (lycopene ε-cyclase), and crtRB1 (β-carotene hydroxylase 1) have been pivotal in developing maize with higher provitamin A content. This article reviews the molecular genetics, biochemical pathways, and breeding strategies involved in the development of vitamin A-rich maize, highlighting the successes, challenges, and future prospects of this "golden gene" revolution.

Introduction

Vitamin A deficiency (VAD) affects over 250 million people worldwide, especially children and pregnant women in sub-Saharan Africa and South Asia. As maize constitutes a staple diet in many of these regions, improving its nutritional profile is a strategic solution to combat hidden hunger. Conventional white and yellow maize varieties contain low levels of provitamin A carotenoids (<2 µg/g), which are insufficient to meet daily dietary needs. Biofortified "Golden Maize" offers a sustainable solution by increasing the content of provitamin A carotenoids, notably β-carotene, α-carotene, and β-cryptoxanthin, which serve as vitamin A precursors in humans.

The Carotenoid Biosynthetic Pathway in Maize

Carotenoids are synthesized in plastids through the isoprenoid biosynthetic pathway, beginning with the condensation of isopentenyl diphosphate (IPP) and dimethylallyl diphosphate (DMAPP). The crucial steps in maize carotenoid biosynthesis include:

1. Phytoene synthase (PSY1) catalyzes the first committed step, converting geranylgeranyl diphosphate (GGPP) to phytoene.

2. Phytoene desaturase (PDS) and ζ-carotene desaturase (ZDS) lead to the formation of lycopene.
3. Lycopene β-cyclase (LCYB) and lycopene ε-cyclase (LCYE) direct the pathway toward β-carotene and α-carotene branches.
4. β-carotene hydroxylase (CRTRB1) converts β-carotene to β-cryptoxanthin and zeaxanthin.

The balance between these enzyme activities determines the carotenoid composition in maize endosperm. Therefore, genetic manipulation of key regulatory genes—PSY1, LCYE, and CRTRB1—directly influences the accumulation of provitamin A.

The Golden Genes of Maize

PSY1 (Phytoene Synthase 1)

The *psy1* gene encodes a rate-limiting enzyme for carotenoid biosynthesis. Natural allelic variation at *psy1* loci can significantly increase total carotenoid accumulation. Overexpression of *psy1* enhances flux through the carotenoid pathway, increasing β-carotene content in maize kernels.

LCYE (Lycopene ε-Cyclase)

The *lcyE* gene controls the partitioning of carotenoid flux between α-carotene (non-provitamin A) and β-carotene (provitamin A) branches. Favorable *lcyE* alleles reduce ε-cyclization activity, thereby diverting more lycopene toward β-carotene synthesis. Marker-assisted selection (MAS) for *lcyE* polymorphisms has been used to increase β-carotene content up to 3–5 fold in maize endosperm.

CRTRB1 (β-Carotene Hydroxylase 1)

The *crtRB1* gene encodes an enzyme responsible for the hydroxylation of β-carotene to zeaxanthin. Functional polymorphisms in *crtRB1* influence enzyme efficiency; favorable alleles slow β-carotene conversion, leading to its higher accumulation. Introgression of the favorable *crtRB1-3'TE* allele through MAS has resulted in provitamin A concentrations exceeding 15 µg/g in elite maize lines—sufficient to meet up to 50% of the estimated average requirement (EAR) of vitamin A.

Breeding Strategies for Provitamin A Enrichment

Conventional Breeding

Early efforts by the International Maize and Wheat Improvement Center (CIMMYT) and HarvestPlus utilized recurrent selection and phenotypic screening to identify high-carotenoid genotypes. However, due to environmental effects on carotenoid expression, conventional breeding alone was inefficient for rapid improvement.

Marker-Assisted Selection (MAS)

The identification of functional markers for *psy1*, *lcyE*, and *crtRB1* has enabled precise selection of favorable alleles. MAS-based breeding programs have successfully combined these alleles into high-yielding backgrounds, significantly enhancing provitamin A levels without yield penalties.

Genomic Selection and Gene Editing

Recent advances in genomic selection (GS) and CRISPR/Cas9 gene editing provide tools to accelerate genetic gain. Targeted knockout of negative regulators (e.g., *crtRB1* high-expression alleles) or promoter engineering of *psy1* can further enhance β-carotene accumulation. Synthetic biology approaches are also being explored to reconstruct optimized carotenoid pathways in maize plastids.

Biotechnological Innovations: The Golden Maize Revolution

The concept of "Golden Maize" is analogous to the development of "Golden Rice." Transgenic maize expressing *psy1* and *crtI* (bacterial desaturase) genes has demonstrated carotenoid enhancement up to 37 µg/g β-carotene in kernels. However, regulatory and biosafety concerns have limited transgenic deployment. Non-GM biofortified maize varieties, developed through MAS, are currently being promoted in several countries including Zambia, Nigeria, and India, under the HarvestPlus initiative.

Nutritional and Health Impacts

Biofortified maize significantly improves vitamin A status when included in diets of vitamin A-deficient populations. Studies have shown enhanced serum retinol levels and improved visual function in children consuming provitamin A maize-based meals. The retention of carotenoids during processing (nixtamalization, drying, and cooking) remains a key area of post-harvest optimization.

Challenges and Future Prospects

While notable progress has been achieved, several challenges persist:

- Stability of carotenoids during storage and processing.
- Genotype × environment (G×E) interactions affecting carotenoid accumulation.
- Farmer and consumer acceptance of yellow/orange maize in regions where white maize is preferred.
- Integration of multi-nutrient biofortification (vitamin A, zinc, and iron) without yield compromise.

Conclusion

The deployment of "golden genes" such as *psy1*, *lcyE*, and *crtRB1* has transformed the landscape of maize biofortification, offering a sustainable strategy to mitigate vitamin A deficiency. Integration of advanced genomics, biotechnology, and breeding innovations has made it feasible to develop nutrient-rich maize varieties that combine high yield, agronomic performance, and nutritional quality. The "Golden Maize" initiative exemplifies the convergence of molecular genetics and food security goals, paving the way for a healthier and hunger-free future.