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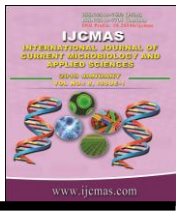

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A Review on Breeding for Quality Protein Maize

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A B S T R A C T

In maize, zeins are the main protein components of seed stores. It is the major determinants of nutritional imbalance when utilized as the sole food source. Zeins having four subfamilies (α, β, γ, and δ). Among these, α zeins are the major prolamin subunits in maize. *Opaque-2 (o2)* is a natural recessive mutation that is exploited for breeding varieties. However, it possessed some adverse pleiotropic effect so, the combination of*opaque*-2 allele with its genetic modifiers composed to breed QPM genotypes that having a hard kernel with a high content of lysine and tryptophan. However, the biochemical analysis of lysine and tryptophan content is expensive as well as it is endosperm-specific.so, conventional breeding alone is inefficacious for the nutritional enrichment of maize. By using RNAi, it is proved that down regulation of 22kDa α zeins than the 19kDa α component is the biochemical basis of QPM phenotype. Whereas, marker-assisted selection (MAS) provide excellent opportunities for the conversion of elite normal in breds to homozygous recessive *o2*forms by using *opaque-2* gene-specific markers.

Introduction

Maize (*Zea mays* L.) is the third major cereal crop in the world after wheat and used for both human consumption and livestock feed. It is known as the queen of cereal crops with the highest grain yield potential. Millions of people in the world acquire a part of their protein and daily calorie requirements from maize. It also has other industrial and non-industrial uses. Maize grains contain nearly8-11% protein (1). The major fraction (60%) of seed protein in maize is zeins (a prolamin group-alcohol soluble) (2) followed by glutelin (34%), while albumin and globulin appear in trace amount (3% each) (3)(5). However, it is deficient in certain essential amino acids, especially lysine and tryptophan like other cereals. A balanced nutrition is necessitated for the proper functioning of the body and its systems and problem of malnutrition is arise if amino acid balance and daily protein requirement are not fulfilled. To extenuate this problem, protein content should be increased and it can be achieved by increasing the prolamine (zein) fraction in maize endosperm (4) However, consequently it leads to lysine and tryptophan deficiency. Thus, it is worthy to follow a genetic enhancement strategy in which essential

amino acids are either assimilated or increased fraction of grain which contains proteins. Momentous progression has been achieved in genetic enrichment of crop plants for nutritional value. In this context, breeding of Quality Protein Maize (QPM)assumes significance for increasing lysine and tryptophan content and reducing the leucine content which helps to balance leucine: isoleucine in the endosperm which ultimately liberates more tryptophan that helps to combat pellagra(5).In this pursuit, this paper deals with the prominent series of events accompanied with the development of QPM, mechanism of *o2* mutant and problem associated with *o2*mutant, the present interpretation of genetic, biochemical and molecular basis of QPM, that could potentially elevate the efficiency of QPM breeding as well as to get efficient QPM cultivars.

Structure of maize kernel

Maize kernel mainly consists of three parts: pericarp (6%), embryo (12%) and endosperm (82%).The pericarp is the outer covering of the kernel that protects and preserves the nutrient value inside of it. A thin, suberized nucellar membrane acquired from the outer epidermal wall of the nucellus persists as a continuous covering between the aleurone and the pericarp. The embryo is located in one face of the basal part of the kernel. A mature embryo is comprised by the embryo axis and the scutellum. Both the embryo and endosperm contain proteins but the germ proteins are superior in quality as well as quantity. Most of the volume and weight of the kernel is accomplished by the endosperm. It can be divided into three parts: starchy endosperm, aleurone layer, and the basal transfer layer (Fig. 1). The aleurone layer is the outer most layers secreted by specialized cells, rich in hydrolytic enzymes. Starch-rich endosperm is present within the aleurone layer having vitreous and starchy regions. The zein proteins form insoluble accretions which are acquired in a vitreous region called protein bodies in the lumen of rough endoplasmic reticulum and it is densely packed between starch grains towards maturity (6). Zeins are the prolamins of maize grain which are soluble in an alcohol having one major class (α-zeins) and three minor classes (β, γ, and δ). These four types constitute about 50-70% of maize endosperm and are essentially rich in glutamine, leucine and proline and poor in lysine and tryptophan (7)(8). Higher proportion of leucine (18.7%), phenylalanine (5.2%) isoleucine (3.8%), valine (3.6%) and tyrosine (3.5%) are normally present in zein fraction, while other essential amino acids such as threonine (3%), histidine and cysteine (1%), methionine (0.9%), lysine (0.1%) are in smaller amounts and is significantly deficient in tryptophan as it is devoid from the major prolamin fraction (α-zeins) of maize kernel. Non-zeins include other proteins such as globulins (3%), glutelins (34%) and albumins (3%). The non-zein protein fraction is balanced and rich in lysine and tryptophan (8).

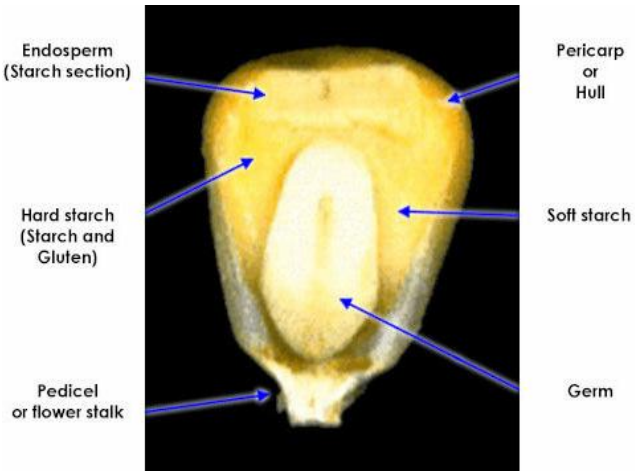

Figure 1. Structure of the maize kernel (Source:

History of QPM

Breeding for improved protein quality in maize commence in the mid-1960s with the

discovery of mutants, such as *opaque-2* (*o2*), Researchers discovered that protein present in endosperm of *o2*maize is nearly twice nutritious compared to normal maize (9) due to elevated levels of lysine and tryptophan that are the two amino acids deficient in maize endosperm proteins. However, successful utilization of these mutants is not achieved due to some adverse pleiotropic effects. So, researchers use two genetic system 1. Exploiting double-mutant combinations and 2. Simultaneous use of *o2*gene and the genetic modifiers of the *o2*locus. However, there was certain drawback like double mutant combination were not always vitreous (10) and yield was severely affected due to the sum total of independent negative effects of two mutation. While the second approach was most successfully adopted. In this, the conservative approach was accepted at the beginning in which after getting certain increment in the level of lysine maintenance rather than further enhancement was adopted and then research diverted towards the development of grain texture. After that QPM donor stock generated by using two strategies: The first was intra population selection for genetic modifiers in *o2*backgrounds elucidates a higher frequency of modified *o2*kernels. In the initial cycle controlled full-sib pollination was executed followed by modified ear-to-row system (8) (11). A selection was accomplished at all stages for modified ears and modified kernels (5)(8) (12).The second approach includes recombination of superior hard endosperm *o2*families.The yellow and white families were recombined separately to develop 'Yellow H.E.*o2*' (yellow, hard endosperm *o2*) composite and 'White H.E.*o2*' composite, respectively. After that large-scale QPM germplasm developed for different zones but standard back cross programme might not work due to the complexity and nature of kernel modification trait. Therefore, an innovative breeding procedure, 'modified back crossing-cum-recurrent selection was contrived for precisely handle the conversion programme as hastily as possible (13) (14)(15). By using this procedure several advanced maize populations in CIMMYT were successfully transformed into QPM populations. Therefore, such collaborative research endeavors bring about refinement of the negative features of the *opaque-2* phenotype, and the outcome is 'Quality Protein Maize' (QPM) that having superior nutritional and biological value and is substantially interconvertible with normal maize in cultivation and kernel phenotype.

Mechanism of *o2* mutant

The binding site for the *o2* protein (*o2*) in the promoter of 22kDaα zein genes are identified and that sequence is similar to the target site recognized by "basic leucine zipper" (bZIP) proteins (5) (16). The promoter regions contain an ACGT core that is necessary for DNA binding and is placed in the -300region respective to the translation initiate. It remains in the highly conserved zein gene sequence motif about 20 bp downstream known as the "prolamin box" (17)(18). When the mutation occurs by *o2* mutant expression of 22kDaα-zein is reduced, that is majorly present in the central region of protein body and this ultimately reduced the size of protein bodies and give soft kernel texture. (19) (20).

The lysine-ketoglutarate reductase (LKR) enzyme activity was examined in two maize inbred lines which having homozygous normal and *opaque-2* endosperms. By examining the pattern of LKR activity outcome was that LKR is correlated with the rate of zein accumulation during endosperm development that was recognized in the *opaque-2*and normal endosperm for the LKR activity. Both were two to three times lower in*opaque*-2 compared to the normal. Due to the reduction in the enzyme activity it

ultimately increases the free amino acid in the endosperm. *Opaque-2* gene may be implicating the regulation of the lysine-ketoglutarate reductase gene in maize endosperm. In accession, lysine concentration was increased in part in which reduction in the reductase activity induced by the *opaque-2* mutation was detected (21) (22).

Problems associated with *o2* Mutants

Opaque-2 mutant having high lysine content brought about enormous interest and eagerness for their possible use in developing maize with superior protein quality. Even though its superior quality, its extensive acceptance is limited and it is also not commercially utilized because of its negative pleiotropic effects include reduced yield than normal maize, low grain consistency and a farinaceous endosperm that retains water (23)(24).

These features result in a soft, chalky endosperm that dried slowly making it prone to damage, a thick pericarp, more susceptibility to diseases and pests, higher storage losses and also affects harvest ability. Since the kernel weight is reduced due to less density per unit volume as starch is loosely packed with abundant air spaces, there is an equivalent decrease in the yield (25).

Especially in developing countries, where farmers are habituated to hard flint and dent grains, the kernel appearance of such mutants formed it less ideal for large-scale utilization and acceptance in target areas. The mutations that alter grain protein synthesis cause changes in the texture of grains.

The early *opaque-2* (*o2*) mutants had reduced levels of α-zeins resulting in small unexpanded protein bodies (26) (27), whereas, *o15* that reduces γ-zeins leads to a smaller number of protein bodies. Other mutations such as *floury-2(fl-2), Mucronate (Mc)* and defective endosperm (*De B30*)result in irregularly shaped protein bodies.(28) (29)

Genetics of high lysine and tryptophan maize

The development of high lysine/tryptophan maize involves manipulating three distinct genetic systems: 1. The simple recessive allele of the *o2* gene: The presence of *o2* in the homozygous recessive condition is mandatory. The most abundant proteins in the grain endosperm are the zeins and, particularly, α zein which is poor in lysine and tryptophan (30). The homozygous *o2*mutant causes a declined in the production of α zein fraction of endosperm protein and an equivalent increment in the fraction of non-zein proteins that naturally contain higher levels of lysine and tryptophan (5).

Modifiers/enhancers of the*o2o2*-containing endosperm to confer higher lysine and tryptophan: It consists of minor modifying loci that influence lysine and tryptophan levels in the endosperm. Lysine levels in normal and *o2*maize average 2.0% and 4.0%, respectively, of total protein in whole grain flour. However, across diverse genetic backgrounds, these levels range from 1.5-2.8% in normal maize to 2.6-5.0% in their *o2*converted counterparts (31). Therefore, continuous monitoring of lysine and tryptophan levels is required.

Genes that modify the *opaque-2*-induced soft endosperm to hard endosperm: Role of gamma zeins to retain hard endosperm phenotype, given that the *o2* modified (hard endosperm) grains have approximately double the amount of gamma-zein in the endosperm compared to the *o2* only mutants(8) (32). To verify the role of gamma-zein in endosperm hardness, RNA interference technology is used in which knocked down of 27 and

16kDaγ-zein genes are accomplished as they are highly conserved in DNA sequence (27).For that two different QTLs are identified as a candidate for *o2* modifier genes. The first is associated with increased expression (33) and the other is linked to *o15* at a different chromosome which causes decreased27kDa γ-zein expression (5) (34).Elimination of γ-zeins obstructs endosperm modification by *o2* modifiers. Partial opacity occurred when the 27 and 16kDa γ-zeins were knocked-down by γ RNAi.It was strongly intensified when the γRNAi and βRNAi both were combined (27). The opacity was caused by an incomplete embedding of starch granules in the vitreous area not by reducing the thickness of the vitreous endosperms. (27) (35). Because the expression of the β-zein gene is also regulated by *o2*(27) (36) and it significantly reduced in QPM (5) (37), the amount of γ-zeins would become critical to keep starch granules embedded in the vitreous area.

Molecular analysis of QPM

A complex antiserum formed contrary to the soluble protein fraction and utilized it in ELISA to determine the level of non-zein proteins in the normal and *o2* endosperm. Even though the correlation between lysine and non-zein content was found to be high (r2 = 0.5), the detail examination indicated that specific lysine-rich proteins in the non-zein fraction may be accountable for much of the variability in lysine content of maize endosperm (38) (39). From the analysis of cDNA clones, a gene-coding elongation factor-1 α (EF-1 α) has been recognized and its synthesis is significantly increased in *the o2*endosperm. (6) (40) EF-1 α is a lysine-rich protein (10% lysine) that is vastly abundant in eukaryotic cells and seems to be incorporated in multiple cellular processes (41) (42).RNA interference technology used for γ zein knock down. During endosperm development, starch granules and protein bodies are immersed in a proteinaceous cytoskeletal matrix (35) (43) (44). The proteinaceous matrix is almost totally absent in *o2* endosperm, resulting in loose and noncompacted starch granules, when in fact in QPM, a matrix is partially restored (35)(43). However, the partial matrix was nullified by knockdown of γ-zeins. Although protein bodies size, number and proteinaceous matrix were all reduced in QPM compared with wild-type endosperm. The normal background revealed round and discrete protein bodies. *o2* developed protein bodies with reduced density and size while in QPM line the number and size of protein bodies were assuredly larger than those in *o2*(35) (45). It could be further confirmed under the scanning electron microscope. When γ-zeins were knocked down, the protein bodies were slightly irregular in size and morphology (35).The higher level of γ-zeins form disulphide bond mediated cross-linking of 27 kDa γ zeins with other cysteine-rich proteins are thought to initiate the formation of protein bodies. There is down-regulation of α, β and γ zein has occurred. There is reduction in 22kDa α and19kDa αzeins in *o2* compared to normal type and 15 β zein is also reduced in the SDS-PAGE analysis of zein proteins. While an increase in non zein fraction in *o2* compared to normal which is rich in lysine and tryptophan. The decrease in 22kDa α zeinsis reported to cause *opaque* phenotype exceedingly as compared to 19kDa αzeins component. This is probably due to the greater interaction of 22 kDa αzeins components with β and γ-zeins resulting in a disruption in protein body formation which causes the *opaque* phenotype (27) (46) (47) (48).

Zeins are synthesized in developing normal maize endosperm between 10 and 45 days after pollination (DAP). At 12 DAP, the19 kDa α and 22 kDa α zeins and *27* kDa γ-zein were detected in SDS-PAGE (49). α zeins

were present in the highest concentration at14 DAP especially19 kDaα is the most abundant. The staining intensity of the27 kDa γ -zein protein was similar to that of the22 kDaα zeins at 28 DAP in the normal endosperm. The27 kDaγ zein was detected abundantly at 12 DAP, while theα zeins, were reduced significantly. The19kDaα proteins were not detected until 14 DAP and 22kDa αzeins were found in only trace amounts in the *o2* endosperm. So, *o2* mutant cause reduction and delayed in the synthesis of α zein (5) (50). To characterize the effect of *opaque-2* modifier genes on γ -zein synthesis and gene expression analysis of normal, *opaque-2* versions of the inbred line and the modified *opaque-2* mutant and their direct and reciprocal F_1 hybrids was developed. Increase in γ zein content in reciprocal crosses compared to direct crosses in both the crosses of normal and*o2* as well as normal and Mo *o2*was observed. This was occurred due to dosage effect (45).*opaque-2 modifiers* act in a semi-dominant manner and are independent of the *opaque-2* genotype (5)(18)(51). Normal, *opaque-2* and QPM Immunostained with αzein antibodies. In normal staining, deposits were absent from the aleurone but they were uniform throughout the endosperm and surrounding the starch granules. Substantially, more immunostaining was observed for normal than with *o2*, QPM. In *o2*, immunostaining is near the peripheral region of cells, adjacent to cell walls. In QPM, staining deposits were uniform throughout the endosperm and surrounding the starch granules. Comparison of this sections stained with antibodies against the γ-zein. In normal endosperm, staining was most intense in the layers of cells adjacent to the aleurone and surrounded the starch grains. Little γ -zein was detected in cells farther away from the first several subaleurone cell layers. The γ -zein distribution in*o2* was similar to that in its normal endosperm. In QPM amount and distribution of γ -zein protein is strikingly different from either of the normal genotypes and *o2*. In QPM, intense staining of γ-zein in the cells was observed just beneath the aleurone layer and extended towards the central region of the endosperm and the intensity of the reaction is even throughout these cells(45).

Marker-assisted breeding in QPM

There is a need of marker-assisted selection because of mainly three reasons: (1) each backcross generation needs to be selfed to identify the *opaque-2* recessive gene and a minimum of six backcross generations are required to recover satisfactory levels of recurrent parent genome (2) To maintain the homozygous *opaque-2* gene, multiple modifiers must be selected. (3) Rigorous biochemical tests to ensure enhanced lysine and tryptophan levels in the selected materials in each breeding generation require. After the sequencing of the maize genome has been completed, a large number of the market system are now available that are associated with *o2*and endosperm modification phenotype (24) (52) (53). A convenient utilization of such markers will greatly enhance the efficacy of selection for improvement of grain protein in maize furthermore reduce the cost and time. Both foreground MAS and background MAS can be efficiently utilized for selecting *o2*phenotypemoreoverassuring maximum recovery of the recurrent parent. MAS used for development of QPM parental lines and developed QPM hybrid in less than half the time required through conventional breeding (24) (31) (54). Various markers are used to introgress *o2*gene intoelite maize inbred lines by rapid backcross conversion programme. They found that using a marker for QPM and endosperm modification can enormously improve the selection efficiency for isolating fully modified kernels in QPM background (55).

In conclusion, quality protein maize has a vast influence on nutritional security with the discovery of *opaque-2* mutation. This natural recessive mutation causes alteration in amino acid composition and *opaque* phenotype of endosperm by regulation of specific zein genes. Modified marker assisted back cross breeding used to develop QPM versions of normal maize inbreds with desirable endosperm characteristics and seed yield. These QPM introgression lines may be united to develop QPM hybrids.

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